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LOCAL DISTRIBUTION OF GRASSHOPPERS IN RELATION TO PLANT ASSOCIATIONS.

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I. INTRODUCTION.

During the summer of 1912, while at the biological station of the University of Michigan, at Douglas Lake, the writer found opportunity to study the relation between local distribution of grasshoppers and the plant associations. The group studied includes the three subfamilies *Tryxalinæ*, *Œdipodinæ*, and *Acridiinæ*, of the orthopteran family *Acrididæ*.

Habitat-distribution of *Orthoptera* has received considerable attention. Published accounts of *Orthoptera* contain the bulk of the data on habitats. The studies of Morse ('04), and of

Hancock ('11), classifying these insects on the basis of habitat, have been reviewed by Shelford ('12*b*: 352). Biological surveys of certain regions, as the Michigan surveys, have included local distribution of grasshoppers (Adams, '06, '08; Ruthven, '11; Hart and Gleason, '07). Studies of animal communities have included data on grasshopper distribution (Shelford, '12*a*; Vestal, '13*b*). In these two studies not all of the associations of the region were considered. In many of the above accounts the concept of the plant association as a habitat has appeared incidentally or not at all; this concept was used in a study of local distribution of birds, by Gates ('11). In the present study all the plant associations of the region have been included, and the plant association has been used as the index of the habitat. In general the results indicate that the important factors of local distribution are, in initial stages of development of the vegetation, *physical* conditions of the environment; in advanced stages, *vegetational* conditions; in either case, the character of the plant association is the index to local environmental conditions for grasshoppers. Collection data are in another paper (Vestal, '13*a*).

Physiography of the Region.

Douglas Lake is situated less than twenty miles south of the northern tip of the southern peninsula of Michigan, in Cheboygan county. There are two main physiographic types, the first being old beaches and lake bottoms of the Nippissing and Algonquin Lakes, and the second morainic in origin. The soil of the first type is almost pure sand; the relief is very slight. The morainic lands have typical rolling topography; they are of mixed composition, usually with loam or sandy loam surface soil. Streams are small and few, but on the whole the region is well drained, the soil being porous. Swamps occupy a very small proportion of the area, and are usually drained. Undrained swamps are few and small in the immediate vicinity.

The lake is about four miles long, with irregular contour, and lies north of a chain of lakes which in recent geological time connected Lakes Michigan and Huron. Douglas Lake was itself, previous to this time, a part of the connection. Much of the shore line is sandy beach, with occasional sand-bars and spits,

and in several places lagoons. Wave action is considerable on exposed parts of the shore-line, but the exposed sand has been very little acted upon by wind. Beach dunes occur sparingly and are of small area.

General Character of the Vegetation.

Much of this part of Michigan is covered with two general types of vegetation, which give rise to the common terms "pine lands" and "hardwood lands." The pine forests have been developed on the more sandy areas, the hardwoods on the loamy or clay moraines. "Hardwood lands" are of much greater agricultural value, and the more extensive farming districts are in morainic regions. The pine lands have been largely deforested, and fire has also been very prevalent, so that many of the original pine forests have been replaced by growths of the large-toothed aspen. In the immediate region of the biological station virtually no pine forest remains, though scattering growths of pitch pine are not rare along the beach, and a few pines are to be found scattered among the aspens. The aspen forest occupies more than one half of the entire area studied; the hardwood forest and hardwood clearings somewhat more than a fourth of the area, and other kinds of vegetation considerably less than one fourth. These other kinds of vegetation are grassland areas, cultivated fields, meadows and sedge growths, cedar bogs, and open peat bogs. The plant associations have been studied in detail by Gates ('13), with reference to a much larger area than has been covered in the present study.

II. The Plant Associations and the Grasshoppers which Occur within Them.

Associations of two vegetation regions or *vegetation provinces* (Gleason, '10: 42–45) occur within the area. The coniferous forests, the aspen forests, heaths and bogs of the region, typical of the northeastern states and much of Canada, represent the *Northeastern Conifer Province.* The deciduous forest (hardwoods) and the herbaceous and thicket growths of hardwood clearings represent the *Eastern Deciduous Forest Province.* While primarily consisting of these two geographic elements, the vegetation also includes *local associations,* particularly those

determined by local conditions of moisture; these are usually not characteristic of any one vegetation province; and *ruderal associations*, composed of introduced plants. Plant names used are those of Gray's Manual, seventh edition.

Associations of the Northeastern Conifer Province.

The culminating type of vegetation in the Northeastern Province is the balsam-spruce-birch forest, which is developed successively through lichen, heath, and different pine stages, in xerophytic situations; and through bog and bog-forest stages in water and wet ground. Only those associations are listed which are represented by distinct areas in the region studied.

Chamædaphne Association (Gates, '13: 57).—No grasshoppers were taken in the open bogs of cassandra. In Ontonagon county, northern Michigan, thickets of cassandra, alder, wax myrtle, high-bush cranberry, etc., are the habitat for *Podisma glacialis* and *Melanoplus islandicus* (Morse, '06: 70).

Thuja Association (Gates, '13: 66).—The cedar or arbor-vitæ growth known as Rees's bog, near the shore of Burt Lake, south of Douglas Lake, was studied. In this bog the peat soil is less than two feet deep, the substratum being sand or gravel. It is drained through the porous soil into Burt Lake. No bare soil is exposed, but partly moss-grown logs lying upon the surface are not infrequent. Trees are usually not more than twenty feet in height, but are close together, and cast a deep shade. *Thuja occidentalis* is the dominant species; *Larix laricina*, tamarack, and *Picea mariana*, black spruce, occur sparingly. The surface is a thick carpet of *Sphagnum;* many peat-bog plants, as *Cornus canadensis*, orchids, ericads, etc., are present, more abundantly in less shaded parts. The only grasshopper species taken in this bog is *Melanoplus islandicus*.

Aspen Association (Gates, '13: 77).—The extensive sandy pine lands of the region are now, as a result of fires and cutting, practically all occupied by the aspen forest. The dominant tree is the large-toothed aspen, *Populus grandidentata*. Other frequent species are paper birch, beech, red oak, hard maple, red maple, wild cherry, *Prunus pennsylvanica*, white pine, pitch pine. The undergrowth, quite similar to that of the pine forest, is chiefly composed of bushy blueberry plants, *Vaccinium penn-*

sylvanicum, which are close together and usually less than six inches high, and of the taller and less numerous plants of the bracken fern, *Pteris aquilina*. Other plants are the bush honeysuckle, *Diervilla lonicera*, and several grasses and composites. Near the lake beach patches of bearberry, *Arctostaphylos uva-ursi*, and of dwarf juniper, *Juniperus horizontalis*, form small heaths. Over all the open aspen growth, a considerable proportion of bare sandy soil is exposed, in the interspaces between plants. Dead leaves, partly decayed and partly burned stumps and logs, litter the surface. There are a number of bare roadways.

The tree growth is irregular, being entirely absent in frequent local areas which vary in size from small unshaded patches between trees to areas thirty meters in diameter. In such places there are indications that the undergrowth is practically independent of the trees. In the older tree growths the hardwood species have assumed control, indicating development into hardwood forest. Ground conditions are more like those of closed forest.

In the treeless parts of the association, in the bracken-blueberry growth, *Melanoplus angustipennis* is the common grasshopper species. *Melanoplus atlanis* and *Camnula pelludica* are common, and *M. bivittatus* occasional, along roadways. *M. luridus* is found sparingly in scattered aspen growths. *Scirtetica marmorata* occurs usually on or near the lichen-covered surfaces. *M. fasciatus* is more often found in the closed forest. On the sandy roads, and sparingly in the sandy interspaces between the plants, are found *M. atlanis*, *M. angustipennis*, *Dissosteira carolina*, *Spharagemon bolli*, *Circotettix verruculatus*, *Arphia pseudonietana*, *Hippiscus tuberculatus*.

Associations of the Eastern Deciduous Forest Province.

The most highly developed form of deciduous forest vegetation is the beech-maple or beech forest, well represented in the region. This develops, on dry soil, through herbaceous, thicket, and xerophytic oak stages, usually, followed by mesophytic red oak and maple stages. The following associations were studied in the Douglas Lake region:

Herbaceous Associations (Gates, '13: 75).—The common fireweed, *Epilobium angustifolium*, is the first plant to establish itself

on newly cleared or burned hardwood land. The clearings are soon overgrown with herbaceous plants, many of them introduced, as mullein, *Verbascum thapsus*. These burns and clearings vary considerably both as regards physical conditions and plant composition. They are only temporary stages in the process of reforestation. Usually they are dry and hot, being fully exposed to the sun, but often sheltered from wind by surrounding forests. Grasshoppers are numerous, both in individuals and in species. In approximate order of abundance they are: *Melanoplus atlanis, Camnula pellucida, Dissosteira carolina, M. bivittatus, Spharagemon bolli, Circotettix verruculatus, M. luridus, Chloealtis conspersa, M. minor*. Only the first two occur in any considerable abundance.

Thicket and Bramble Associations (Gates, '13: 76).—The shrubby plants which replace the herbs in clearings are principally blackberry and raspberry, *Rubus* spp., red-berried elder, *Sambucus racemosa*, and young seedlings and shrubs of hard maple, *Acer saccharum*. These growths often form a dense tangle which is almost impenetrable. In dense parts of these thickets an occasional *Melanoplus bivittatus* would be seen upon a leaf at the top of a shrub. Where the ground could be seen, *Melanoplus atlanis, Camnula pellucida*, and *Chloealtis conspersa* were also to be found.

Beech-Maple Association (Gates, '13: 71).—The beech-maple forest is dominated by two tree species, *Fagus grandifolia*, which occurs in places in nearly pure stands, and *Acer saccharum*. *Tsuga canadensis*, the hemlock, is also important in places. *Ostrya virginiana, Betula lutea*, and *Tilia americana* are infrequent species. In the deeply shaded parts of the forest, the undergrowth consists mainly of young seedlings of *Fagus* and *Acer*, with small plants of *Maianthemum canadense* and *Mitchella repens*, partly hidden in the thick carpet of fallen leaves. In the sunlit spots the undergrowth is taller, with *Acer pennsylvanicum* and *Sambucus racemosa*. Many other forest plants occur. Stumps and logs are common, but no bare ground is exposed. The relative humidity is high. Exposure to sun and wind is at a minimum. *Melanoplus islandicus* is a characteristic grasshopper species, of the deeply shaded parts of the forest. It is probable that *Podisma glacialis variegata* occurs also on shrub-

bery. In more open parts of the hardwood forest, and near the edges of clearings, most of the grasshopper species that are common in clearings were also found, in very small numbers, however.

Ravine Forest Association (Gates, '13: 66–70).—This association is best developed in the ravine occupied by what is locally known as *Big Springs*. A number of springs, fed by the underground drainage from Douglas Lake, to the north, form the head of Carp Creek, which runs south to Burt Lake. The ground is very wet, and is occupied by bog plants and deciduous forest undergrowth. Trees are *Tilia americana*, *Tsuga canadensis*, *Fagus grandifolia*, *Ostrya virginiana*, *Betula lutea*, *Acer saccharum*, *Abies balsamea*. Succession has proceeded from the coniferous bog forest toward the beech-maple association. *Podisma glacialis variegata*, recorded from Carp Creek, probably was taken in this ravine forest, *Melanoplus islandicus* probably also occurs in the same association.

Local Associations.

Dry Beach Associations (Gates, '13: 55).—Quite a number of the strand plants of the sandy margins of Douglas Lake belong to an assemblage which is characteristic of the sand shores of the Great Lakes. Three of these independently form associations in the region. These are *Elymus canadensis*, *Ammophila arenaria*, and *Potentilla anserina*. *Elymus* forms a low, narrow dune about one eighth mile long, at the southeastern end of the lake. It and *Ammophila* are found just above the level of wave action at many places on the shore. Sandbars on the north shore were partly covered by *Potentilla* growth. In these beach associations the soil is pure sand, dry and shifting, with full exposure to sun and wind. The vegetation is dry and scanty. Grasshoppers typical of these situations are: *Melanoplus atlanis*, *M. angustipennis*, *M. bivittatus*, *Camnula pellucida*, and *Dissosteira carolina*. Two species not taken at Douglas Lake, *Spharagemon wyomingianum* (Thomas), and *Trimerotropis maritima* (Harris), are very characteristic of beaches and dunes of the Great Lakes; both are recorded by Shull from the Saginaw Bay region ('11: 225–226).

Marsh Associations (Gates, '13).—Communities of marsh

plants bordering lakes, streams, and certain open bogs are usually composed of only one or a few plant species. These growths, depending upon local conditions of moisture, are frequently small in area, and different stations are not always alike. Conditions of shade and of soil are variable. No grasshoppers were found upon the marsh plants which grew standing in open water, although in dense growths individuals sometimes stray beyond the shore. The numbers of grasshoppers vary considerably in different stations. They are most numerous in tall, rather close, sedge or grass growths. *Stenobothrus curtipennis* is the characteristic grasshopper of littoral situations. *Melanoplus atlanis*, *M. bivittatus*, and *M. differentialis* are less frequently found. *M. femur-rubrum*, though not taken by the writer, is often found in such places. The *Melanopli* are more numerous in the higher and more open parts, while *Stenobothrus* occurs farthest out towards the water.

Ruderal Associations.

In the Douglas Lake region much of the native forest has been removed by cutting and burning, and its place has been taken by cultivated crops and weed growths. In addition many plant associations, though not destroyed, have been materially changed, and native animals have also been much affected. Secondary successions are principally due to interference by man. Most of the sandy land is now occupied by aspens as a result of destruction of the pines. One of the most important plants favored by artificial conditions is the blue-grass, *Poa pratensis*, which enters into nearly all ruderal growths. Other species of *Poa* probably occur in the region.

Ruderal Dry Grassland Associations.—Abandoned fields, dry pastures, roadside growths, and modified aspen undergrowth are the common forms of ruderal growth in dry situations. They are necessarily very different in physical conditions and plant composition, depending upon differences in original status and subsequent modification. In certain large areas west of Douglas Lake, near Pellston, a growth of bluegrass has almost entirely replaced the aspen association. Near the lake bluegrass invades the aspens along roadways, and one can trace long abandoned roads by the presence of this plant. Other weed species are

numerous. Grasshopper species of ruderal dry grassland are, in approximate descending order of importance: *Melanoplus atlanis*, *Camnula pelludica*, *M. bivittatus*, *Dissosteira carolina*, *Arphia pseudonietana*. All of these species, with the possible exception of the last, are more abundant in ruderal than in native vegetation.

Sparsely Vegetated or Bare Soil.—The condition of bare soil is much more frequent, in humid climates, as a result of disturbance. Plowed fields and constantly trampled paths and roads are the commonest areas of bare soil, and these furnish suitable habitats for those species which normally rest on bare soil, not on the plants. The *Œdipodinæ* are of this habit to a large extent. The character of the soil is important for oviposition, and though the bare soil grasshoppers are more or less migratory, certain of them are found associated with particular types of soil. Hart gives the soil-preferences for a number of the *Melanopli* in a sand region in Illinois ('07: 214, 215). It is to be remembered that bare soil as a habitat is not sufficient; nearby vegetation is necessary, and in this region is always present. Where extensive areas of bare soil occur, grasshoppers are very rare except at the border. The insects are conspicuous in bare places, as roads, but are more abundant in the interspaces between plants, in open growths. Areas of bare soil differ from the sparsely vegetated areas merely in degree, and are really the same kind of habitat. In the region studied considerable bare soil is exposed along the beach, but in the aspen association roads are the typical areas of bare and sparsely-grown soil, as also in the hardwood district. Interstitial grasshoppers which are conspicuous in bare soil are: *Dissosteira carolina*, *Arphia pseudonietana*, *Circotettix verruculatus*, *Spharagemon bolli*, and *Hippiscus tuberculatus*. Those of open grassland, frequently found on bare soil of interstices, and less frequently on bare soil of roads, are: *Camnula pellucida*, *Melanoplus atlanis*, *M. bivittatus*, *M. angustipennis*.

Meadow Associations.—Ruderal meadows and swales, like the native marsh and littoral associations, are variable in character. Probably the most common type is the bluegrass-white clover meadow. It is found in wet pastures and along boggy roads; it forms a very low, dense carpet, resembling a closely trimmed lawn, and probably always depends on constant cropping of

cattle. It is of common occurrence on the north shore of Douglas Lake, and near Munro Lake, several miles north. In this type of meadow *Melanoplus atlanis* and *Stenobothrus curtipennis* are of about equal abundance. *M. femur-rubrum* was not taken, but is more abundant in such places in other localities than is *M. atlanis*. *M. differentialis* is typical in meadow habitats, and *M. bivittatus* is found sparingly.

Arrangement of the Associations as Habitats.

The associations of any particular region may be placed in groups with respect to several well-known criteria. One of the prevalent methods is to consider together all associations which are genetically related, which form a developmental series, each stage being succeeded by the next in order, until the ultimate or climax association is reached. Another mode of classification is geographic, placing together all associations of like geographic distribution, all typical of a definite climatic region, an ecological province. Another grouping is based upon growth-form: by this treatment associations dominated by plants of similar growth-form, indicating physiological likeness, would be considered similar, regardless of geographic or successional relationships. The common division of associations of a region into climatic or geographic, and edaphic or local, is based upon local distribution or habitat. The grouping into aquatic and terrestrial is a grouping based upon habitat in a larger sense: the medium of life is the important feature. Finally it is necessary to distinguish between primary, original or native associations, and secondary, ruderal or cultural associations, wherever human influence has modified primeval conditions. These different groupings are not at all parallel, but form a complex. To orient an association with respect to others of the same region it is necessary to find its place in this complex. In a regional treatment it is usually necessary to consider all of these criteria. For different purposes, different bases of classification may be emphasized, but in no case should one basis be confused with another.

For the purpose of the present study, in which the plant associations are considered mainly as habitats for grasshoppers, two bases of classification receive emphasis. The first is with respect

to habitat, the second with respect to growth-form of the plants. These two considerations determine the physical and vegetational conditions to which the grasshopper species are subjected.

It is to be understood that grasshoppers are animals of the ground stratum and of the herbaceous stratum. In so far as these strata are similar as habitats in different plant associations, these associations may be treated together. Considerations as to whether associations are proximate or ultimate, geographic or local, native or ruderal, whether they belong to the Northeastern Province or the Deciduous Forest Province, are of interest only as they affect relative area of different associations within the region, and consequently the relative frequency and abundance of the grasshopper species of the different associations. In the following synopsis, the moisture factor is used for the division according to habitat, though other physical factors, such as soil, might have been used if it had been desirable to subdivide further. The synopsis arranges the associations of the region according to their similarity as habitats for grasshoppers.

Herbaceous or grassland associations.
- In wet or moist habitats.
  - Sedge and other littoral associations.
  - Meadow associations.
- In dry habitats.
  - Sparsely vegetated or bare soil.
  - Beach-grass associations.
  - Ruderal dry grassland.
  - Hardwood clearings.
  - Bracken-blueberry growth of open aspen forest.

Forest associations.
- In wet or moist habitats.
  - Cedar bog forest.
  - Ravine forest.
- In mesophytic habitats.
  - Closed aspen forest.
  - Beech-maple (hardwood) forest.

Among the dry grassland associations, variable conditions (resultants of both physical and vegetational agencies) are: texture and compactness of soil, humus content, proportion of bare surface; height, density, and general character of the vegetation. Sparsely vegetated grassland has a high proportion of bare surface; roadways and other small areas of bare soil are to be considered as part of an area of open vegetation.

It should be pointed out that conditions in the ground stratum of the aspen association are the same in the open treeless parts as among scattered trees. Exposure to sun and wind, as well as the vegetation, are almost identical in the two places. The open aspen forest is then, so far as its ground stratum is concerned, *a grassland association*. This is in accord with the results of Shelford ('12*a*: 82), who found that ground stratum conditions in open forests in sand at the lower end of Lake Michigan lag behind in the succession from herbaceous to forest growth. In reality open forests of very scattered trees are usually mixed associations, dominated in places by trees, and in more open places by herbaceous plants. So far as ground conditions are concerned, the association is herbaceous, and the bracken-blueberry growth is accordingly grouped with dry grassland. Ground conditions are not those of forest until the closed stage of the aspen association is reached. The lichen growth of open aspen areas, affording a locally different environment, may be regarded as a minor division of that association.

A primary division in the above synopsis, "shrub associations," might have been added. The thicket and bramble associations were small in area, were little studied, and as the conditions in the ground stratum in thickets are much the same as those in the hardwood forests, with about the same grasshopper assemblage, this division is omitted for simplification.

The grasshopper assemblages of these associations are presented in summarized form in the third section of this paper, which here follows.

III. Summary of Local Distribution of the Species.

The table which follows summarizes the habitat relations of the grasshopper species, and includes an approximate estimate of the numerical status of each species in each of its habitats. The method of numerical estimation is described on p. 165. It is necessary at this point to define the terms used to denote degrees of frequency, or regularity of occurrence, and abundance, or numbers of individuals per unit of area. *Dominant* species in a habitat, usually only one or two, have a very high abundance, and a high frequency, in that habitat. *Abundant* species are also

TABLE I.

SUMMARIZING HABITAT RELATIONS OF THE GRASSHOPPERS OF THE DOUGLAS LAKE REGION.

Terms denoting degrees of frequency and abundance are defined immediately above, and are abbreviated in the table. Question-marks are inserted to indicate probable occurrence in habitats little studied. Where a space is blank it is understood that the species occurs accidentally or not at all in the particular habitat.

	Moist Grassland.		Dry Grassland.					Forest.			
	Sedge Growths.[2]	Wet Meadow.[2]	Bare Soil.[2]	Beach-grass.[2]	Ruderal Grass-land.[2]	Bracken-Blueberry.	Hard-wood Clearings.	Closed Aspens.	Beech-Maple.	Ravine Forest.	Thuja Bog.
Stenobothrus curtipennis (Harris)	Freq.	Freq.		Accid.							
Melanoplus differentialis (Thomas)		Freq.			Freq.	Occas.	?		?		
Melanoplus bivittatus (Say)		Freq.	Infreq.	Occas.	Freq.[1]	Occas.	Freq.		Infreq. or Accid.		
Melanoplus femur-rubrum (De Geer)		Freq.?		?	Freq.?	?	Freq.?				
Melanoplus atlanis (Riley)		Abund.	Freq.[1]	Abund.	Dom.	Freq.	Abund.	?	Infreq. or Accid.		
Camnula pellucida (Scudder)		Accid.	Freq.[1]	Freq.[1]	Dom.	Freq.[1]	Abund.	?	Infreq. or Accid.		
Melanoplus minor (Scudder)							Infreq. or Occas.				
Melanoplus luridus (Dodge)				?	?	Occas.	Occas.				
Melanoplus angustipennis (Dodge)			Occas.	Freq.	Infreq.	Dom.					
Dissosteira carolina (Linnæus)			Freq.[1]	Freq.	Freq.[1]	Occas.	Freq.[1]				
Spharagemon bolli Scudder			Freq.[1]	Occas.		Occas.	Occas.		Infreq. or Accid.		
Arphia pseudonietana (Thomas)			Freq.[1]	Infreq.	Freq.[1]	Infreq.	?				
Hippiscus tuberculatus (Palisot)			Freq.	Infreq.	?	Infreq.	?				
Circotettix verruculatus (Kirby)			Freq.	Occas.	Occas.	Occas.	Occas.		Infreq. or Accid.		
Scirtetica marmorata (Harris)						Infreq.[3]	?	?			
Melanoplus fasciatus (Barnston-Walker)						Infreq.	Infreq.[4]	Freq.[1]			
Chloealtis conspersa (Harris)						?	Occas.	Infreq. or Occas.	?		
Podisma glacialis variegata Scudder									?	Occas.?	?
Melanoplus islandicus Blatchley									Freq.	?	Occas.

[1] Frequently found, usually not in numbers, but in a few places approaching abundance.

[2] Stations representing these five habitats were rather variable as to physical and vegetational conditions, and also as to the numbers and species of the grasshoppers. Data for these five columns were compiled from more detailed tables in which a vertical column was assigned to each station of each of these habitats.

[3] More typical of the lichen-covered surface in more or less sheltered parts of the bracken-blueberry growth. In the association as a whole the species is infrequent; in lichen patches it is frequent.

[4] One specimen of the long-winged form, *M. f. volaticus*, was taken in the grassy border of a growth of hardwoods.

frequent; they are usually to be found in the habitat in considerable numbers at any time. *Frequent* refers to grasshoppers occurring regularly in the habitat, though not always to be found, and seldom numerous when found. *Occasional*, occasionally found in the habitat, not frequent or abundant. *Infrequent*, not often found in the habitat. *Accidental*, occurring in a habitat rare or unusual for the species. Specimens are usually found singly and the abnormal habitat frequently adjoins one in which the species is more regularly found.

The obvious facts shown by the table are:

1. Grasshoppers are more abundant, in species and in individuals, in herbaceous or grassland habitats than in forest, and more abundant in dry than in moist or wet situations.

2. Certain species are much more restricted than others in range of habitats, and in accompanying range of toleration of physical and vegetational factors of the environment.

3. Although a species may be found over several associations, it is more abundant in one, or two, of these, than in others (Certain activities take place in more restricted habitats; chief of these restricted activities is the laying of eggs.)

4. No two plant associations have identical grasshopper assemblages.

5. No two grasshopper species have identical habit-preferences.

These facts and others are considered in order in the general discussion.

In general, with every change of habitat there is a change in the assemblage of grasshopper species. These replace one another in the various habitats, often with considerable overlap, but all can be arranged with respect to gradients of environmental conditions. Gradients of several factors which vary together may in general be said to run parallel with the development of vegetation. This development of vegetation is in part the result, in part the cause, of these changes of physical and vegetational conditions.

The variation of environmental conditions can be expressed graphically by lines representing gradients of the factors which change with development of vegetation. Environmental conditions in each successional series may be represented by a line,

at one end of which the conditions are those of sterile soil or water, environmental control being entirely physical; at the other end conditions are those of the closed, completely developed, climatic association, vegetational control of local environment being nearly complete.

It is further possible to arrange the lines representing the different successional series within a region, so that relations between them may also be seen graphically. Fig. 1 (p. 156) is an arrangement of the gradients of physical and vegetational conditions in the Douglas Lake region, based on the development of vegetation, and accompanied by a representation of the selection of these conditions by the various grasshopper species.

IV. General Discussion.

The Assignment of Terrestrial Animals to Habitats.

It is thought by some zoölogists that the local distribution of most terrestrial animals is more or less haphazard, that there is no order in the distribution of animals into different habitats, or that, if there is order, the conditions of distribution are too complicated to be determined by any present methods. Shelford ('11: 591) points out several reasons for the prevalence of these and similar opinions. On the contrary, environmental relations of animals are now coming to be recognized as quite definite (Shelford, '12*b*: 333).

The habitat, in the sense of abode for animals, is a particular combination of certain environmental conditions, physical and vegetational, and to some extent, animal, uniform over a certain area. More or less variability within this area is the rule, and we may consider the area of the habitat as larger or smaller, according to the degree of uniformity of conditions. In these areas of varying degree, plant and animal communities of various degree find their existence. Ecological classification, aside from its dealings with plant and animal individuals, has to do with the recognition and classification of these degrees of likeness and difference of environments and of plant and animal communities. (See Shelford, '12*b*: 355.) The habitat considered most convenient in the treatment of local distribution of

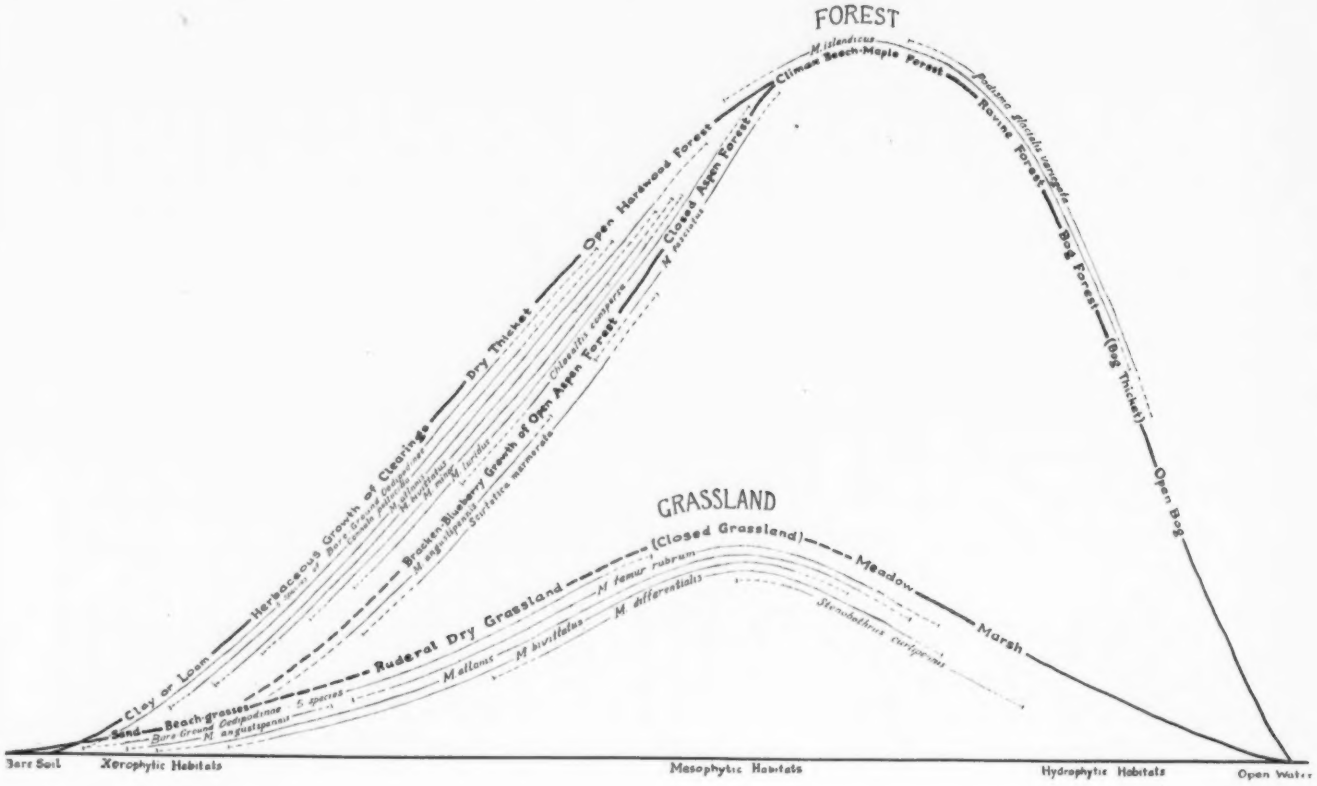
FOREST
M. islandicus
Climax Beach-Maple Forest
Ravine Forest
Bog Forest
(Bog Thicket)
Open Bog
Prunus pumila
Open Hardwood Forest
Dry Thicket
Herbaceous Growth of Clearings
Closed Aspen Forest
M. laevidus
M. avicularis
Bracken-Blueberry Growth of Open Aspen Forest
Chiogenis canescens
M. angustipennis
Sturtevantia saxorosa
GRASSLAND
(Closed Grassland)
Meadow
Marsh
Ruderal Dry Grassland
M. femur rubrum
Mellanus
M. bivittatus
M. differentialis
Stenobothrus curtipennis
Clay or Loam
Sand
Beach-grasses
Bare Ground
Cedipodinae
M. angustipennis
S. spacres
Bare Soil
Xerophytic Habitats
Mesophytic Habitats
Hydrophytic Habitats
Open Water

FIG. 1. Showing the relation between grasshopper species and gradients of physical and vegetational conditions within the Douglas Lake region. At the left are initial stages of vegetation developing from dry ground; at the right initial stages developing from wet ground or open water. Conditions vary as development of the vegetation proceeds; at the top of the curve xerophytic and hydrophytic series converge in the climax association. Vegetational control is, roughly, successively greater from bottom to top. Moisture content is successively higher from left to right. Only the initial stages of grassland vegetation would normally be represented in the region, as forest invasion would prevent development of closed grassland. However, certain ruderal associations within the region present conditions essentially those of partially and of nearly closed grassland, and these associations are accordingly placed in the proper place in the gradient of grassland environmental conditions. Stages not well represented within the region are in parentheses (bog thicket, closed grassland). In certain of the gradients the transition between two stages is not direct, as between beach-grass and open aspen forest. Such indirect transitions are represented by dotted lines. The gradient for development of coniferous forest is not shown; it might be represented by a line parallel to the other dry forest gradients.

Approximate range of the grasshopper species in the various gradients is shown by fine lines, which are dotted in the extremes of the range, in which their occurrence is infrequent and their numbers small. It is seen that certain species occur in equivalent stages of the different kinds of vegetation. Species common to hardwood and aspen forests are placed between the two gradients; those restricted to aspen forest are to the right of the aspen gradient.

grasshoppers within a region is the area marked off by the plant association, in which there is a general and usually recognizable uniformity of vegetation and of physical conditions.

A species is to be assigned to a habitat if its occurrence in that habitat is a matter of regularity. In general, the animal species is seldom confined to a single habitat within a region. The determination of the more typical habitats selected by a particular species involves estimation of relative numbers, and presents certain difficulties, which are discussed below. In a regional study of a group of animals taxonomically related, or of all the animals of the region, there are certain other difficulties which obscure the definiteness of habitat relations.

Variation in Range of Habitats in Different Species.—The range of toleration of environmental conditions varies widely among different species of a taxonomic group, and accordingly we find certain animals restricted to one or several similar habitats, while others range over many and different habitats with apparently little discrimination. *Melanoplus atlanis*, for example, occurs regularly in meadows, in dry open grassland, and in open forest. It is a species which can endure widely varying conditions. Upon examination, it is found that it is very much more numerous in certain habitats than in others, and that there are certain habitats in which it occurs only accidentally or not at all. In the Douglas Lake region, it was never seen in cassandra bogs, in bog or ravine forests, in closed aspen forest, and only infrequently or accidentally in closed hardwood forest. There is, then, a *selection* of habitats, and the local distribution of even the most generally distributed forms is far from indiscriminate.

Habitat-Distribution as Affected by Motility of Animals.—The habitat relations of plants are more evident than those of animals because the plant individuals are non-motile, while animal individuals can move about, and it is not to be supposed that they will necessarily stay within a single area of uniform conditions. They continually stray beyond the limits of conditions necessary for all or part of their activities. Among the grasshoppers, certain are much more motile than others, particularly the long-winged and active *Œdipodinæ*. These grasshoppers at times fly high and to considerable distances, and may be seen to traverse

areas of dry grassland, of marsh, and of forest. However, while at rest, very few will be found on trees, for example, or in deep shade, or in dense herbaceous vegetation. They will usually be seen in open dry vegetation or on bare soil. If found in other conditions, these will usually be not far distant from such open situations. Stray individuals are not common and are usually found singly. It is not surprising that stray individuals should be more frequent among species which are very abundant in the region, as *Camnula pellucida*, and among species of the more extensive habitats. The motility of animals is perhaps commonly overestimated as a factor in width of local distribution. The daily itinerary of an animal is likely to be more circumscribed than is usually thought. In the case of the grasshoppers again, for most species the *ordinary* mode of progression is walking or crawling, rather than jumping or flying. Usually grasshoppers are noticed only when disturbed, or "flushed." Their behavior, jumping or flying *when disturbed*, is a special reaction to an approaching object. The ordinary activities are much less frequently observed. Birds, our most motile animals, have very definite habitat relations (see Gates, '11). Though the actual number of observed occurrences of stray individuals in unusual situations may be large, these occurrences are very infrequent and exceptional when compared with occurrences in the normal habitat.

Differences of Activity in Different Habitats.—Various activities of the animal may take place in different strata of one habitat, or in different habitats, separated horizontally. The stratum or habitat of greatest importance to the animal is the one in which the most narrowly limited activity takes place, and this activity is usually concerned with breeding (Shelford, '07, '11).[1] In the case of the Douglas Lake grasshoppers, eggs are laid just below the surface of the soil, or at least in the ground stratum, and proper conditions for oviposition are among the most important considerations which determine the presence of the particular species in the region, and *the* important consideration in determining which habitat within the region is most essential to the

[1] On p. 595 (Shelford, '11) are given references to other authors, in which instances of breeding activities as being most narrowly limited are given for birds and for fishes.

species. The habitats in which few or no grasshoppers are found are those in which the soil is not suitable for egg-laying.

In many animals the breeding period occupies a rather small part of the season of activity, and the adult animal may spend but a small proportion of its active life in the breeding stratum or habitat. The habitat in which the species occurs most regularly and in the greatest numbers is the habitat in which the species is of greatest influence. It is the most important habitat of the species so far as plants and other animals are concerned. In associational studies, in which emphasis is laid upon relations between organisms, this habitat is most important. The animal may feed in several habitats, but principally in the habitat in which it is most frequent and abundant. The feeding activities, though of secondary importance (usually) in determining the presence of an animal in a particular habitat and a particular region, are of primary importance in relation to the communities of plants and animals of which the species becomes a member. In the study of all the habitats within a given region, emphasis would be placed on the habitat in which the species is most frequent and most abundant. The success of the species in the various habitats, as indicated by relative numbers, is a measure of the degree of correspondence between the environmental conditions actually furnished within the area of the habitat, and those required by the animal. The habitat in which the species is found most regularly and in the greatest numbers is the habitat in that region which most closely approximates the optimum environment for the species.

The Different Activities in Climatic and in Local Habitats.—It so happens, in probably the majority of the grasshopper species of the Douglas Lake region, that the feeding habitats and the breeding habitats coincide more or less perfectly. In insects of incomplete metamorphosis, as *Orthoptera*, the possibility for the immature animals to correspond in mode of life rather closely to the adults is much greater than in insects in which changes from larva to adult are more radical. Grasshopper nymphs feed and hop about as do the adults. They cannot fly, but as flying more commonly does not take the animal into another habitat, this difference is of minor importance. Where the

habitat in which the species is more frequent and abundant is of considerable extent within the region, as in climatic associations, soil conditions, or conditions for egg-laying, would be either uniform throughout the area of the habitat, or else suitable small spots would be scattered about within the area. There would then be no necessity for the females to migrate to a different habitat for oviposition. Thus most of the grasshoppers found in the aspen association would be able to lay eggs within its area, and the nymphs would find food and other necessary conditions in the same place as do the adults. In the beech-maple or cedar-bog forests, which individuals of *Melanoplus islandicus* probably rarely leave, suitable egg-laying sites, in this case wood as found in stumps or logs, are scattered about over the forest floor. It thus appears probable, in the extensive habitats provided in terrestrial climatic plant associations, that the correspondence between the conditions required for breeding and the conditions required for feeding and other ordinary activities, may be quite general. Conditions for egg-laying among insects, for example, may still be more restricted than conditions required for other activities, but the local variability of environmental conditions within the area of the plant association is sufficiently wide, usually, to include the more restricted conditions necessary for egg-laying, or whatever the most narrowly limited activity happens to be. If what is true in the case of grasshoppers is true in a large number of terrestrial animals, as seems likely, this means that the limits of the climatic plant association need not be passed, ordinarily, by a large number of the animal species, since all the necessary conditions are supplied within its area. The animal community of the area may be thus, in large measure, self-contained, and coextensive with the plant community.

In local habitats, on the other hand, which are usually restricted in extent and consequently likely to present less variability of environmental conditions within the area, it is less likely that all the conditions necessary for the animal species will be supplied within the area. The number of animal species which can find all the necessary conditions for existence within the area will be comparatively small; thus many of the species will be obliged to perform certain of their activities in other habitats.

Furthermore, environmental conditions in local habitats are likely to be the extreme, rather than the mean, conditions within the region. Thus sedge marsh habitats in the Douglas Lake region have submerged or very wet soil; in the latter case, the growth may be so dense as to leave no exposed soil. These are extreme conditions for terrestrial habitats. The only grasshopper of the region which was seen in such situations is the ectophytic *Stenobothrus curtipennis*. It is probable that this species deposits its eggs in higher and drier soil. Unlike most of the grasshoppers, its ordinary activities can be carried on in a very humid environment, and the presence of exposed soil is not necessary. The conditions necessary for breeding, however, do not correspond with the extreme condition of wet soil, and must be obtained outside the area of the extreme habitat. The local habitat is less likely to be self-contained than the extensive or climatic habitat.

Difficulties Arising from Habitat Complications.—The habitat relations of animals sometimes are much less evident at the tension zone between two contiguous habitats, and there is the further complication that habitats are sometimes distinguished with difficulty. Boundaries will be invaded by animals of both habitats. The tension zone is much wider, and the confusion greater, between two rather similar habitats. As Shull points out ('11: 221), the determination of habitat relations is difficult in regions where the habitats are small in area and much intermingled. The tension zone presents one great advantage in that it allows determination of which species of one habitat range farthest and most frequently into the adjoining habitat. A graded series of species can be determined, which expresses the resultant of different factors entering into habitat selection of the different species.

Unstable habitats are frequently indicated by the presence of mixed plant associations. These contain representatives from two or more plant communities. Thus near the beach of Douglas Lake, the bracken-blueberry growth is mixed with bearberry and juniper heaths, a few small clumps of beach-grasses, in certain spots, and in others by local growths of ruderal bluegrass. In such mixed areas the animal assemblage is not of the constant character seen in more uniform growths.

Mixed conditions within the area of a habitat also tend to confuse. This is particularly well shown in open forest. *Melanoplus fasciatus* and *Chloealtis conspersa*, of the species studied, are found in open forest with a number of other grasshoppers, but appear to be the only two for which forest conditions are really necessary. All the others are grassland species, and are present because of the grassland environment of the ground stratum. Grassland species may be found in very small sunlit grassy patches within a closed forest. These sunlit patches are not to be considered as part of the closed forest habitat. Probably very few insects of the ground stratum are really typical of open forest.

Roadsides and other local modifications are a source of error in assigning animals to a habitat. A collector traveling along the sandy roads through the bracken-blueberry growth of the aspen forest would see large numbers of bare-ground *Œdipodinæ*, almost all on the roads. He might never realize that these grasshoppers are not particularly common in the undisturbed growth, and that they are animals of the roads and not of the bracken-blueberry growth.

Furthermore, the habitat is not entirely uniform within its area. There are many extremely local environmental differences within the habitat, which influence the animal species as well as the plant species. Thus in scattered parts of the bracken-blueberry growth, occasional patches of lichen-covered surface are found. With these patches is associated the grasshopper *Scirtetica marmorata*. It does not occur over the entire bracken-blueberry growth, as does *Melanoplus angustipennis*, for instance.

Within the habitat there are local differences in the degree of development of the vegetation. This is shown in grassland in the degree of openness of vegetation. Where considerable bare surface is exposed between the plants, bare-soil animals are found. In closed grassland, no animals of this habit occur. Differences of development are shown in the aspen forest. Among scattered trees the bracken-blueberry growth presents an environment essentially that of grassland. In more compact tree growths ground conditions begin to approach those of the forest floor. Only in such situations is the short-winged grasshopper *Melanoplus fasciatus* to be found.

Estimation of Relative Numbers in Different Habitats.

The Distinction Between Frequency and Abundance.—Many collectors do not distinguish between frequency of occurrence and abundance of individuals. To them a species is common if scattered individuals are seen frequently, or if numerous individuals are seen infrequently. Frequency refers to regularity of occurrence in one or more habitats; abundance is concerned with numbers of individuals per unit of area. The distinction is indispensable if we are to estimate numbers of individuals in different habitats. Thus many of the conspicuous *Œdipodinæ*, a number of which can be seen in flight at one time, but over a considerable extent, as far as one can see, are frequent species, but are not numerous as compared with certain inconspicuous *Melanopli*, a larger number of which may be found in any area within the habitat as large as a few meters square. These last are abundant *and* frequent.

Difficulties in the Way of Numerical Estimation.—The writer is not acquainted with any very practicable method of estimating absolute numbers of insects in different habitats of a region. Absolute numbers of plants may be estimated under favorable circumstances, as may also the numbers of the larger or more sedentary animals. Following are some of the difficulties encountered in estimating absolute numbers of terrestrial animals: In any one species, there are differences in numbers of individuals, in degree and kind of activity, in readiness with which it is perceived, in ease with which it is captured, or recognized if it is not taken, in time and in space. These conditions vary with the year, with the season, with weather conditions, and with the time of day; they vary in different habitats, in different strata, with different kinds of soil and against different backgrounds, and in different kinds of vegetation. There are many difficulties in the way of estimating even relative numbers of different species. Less abundant species are likely to be confused with more abundant kinds. There are differences in appearance, in conspicuousness, in degree of activity, in ordinary behavior and behavior upon being disturbed, with different species, which make some of these much more readily perceived, or recognized, or captured, than others. Differences in time of appearance and activity, and

in place, in surroundings, may make certain species appear more or less abundant or frequent than they really are.

The method used by Shull ('11: 218) in estimating numbers of grasshoppers per unit of area is valuable, but does not distinguish the different species. His suggestion "to collect immense numbers, and depend upon majorities to decide the usual habitat," besides being impracticable, is not satisfactory, for the numbers collected are not a true index of the numbers which actually occur by reason of the difficulties mentioned above.

The Method Used in Determining Frequency and Abundance.— The method used by the writer was to visit the various habitats, taking one or several grasshopper specimens of each species for verification, and to estimate abundance not from the numbers collected, but from the numbers observed per unit of area in each station, having in mind the considerations which tend to over- or underestimation of actual numbers.[1] If in the bracken-blueberry growth, a considerable number of *Melanoplus angustipennis* could be seen nearby, within a rod or two, and if this condition was practically uniform over the area of the association, as nearly as could be seen, an infinity sign was put down in the field notes opposite its name, indicating numbers in which it occurred, followed by the number collected, thus (∞, 2). If in twenty minutes walk through the aspens only four or five specimens of *Scirtetica marmorata* were seen, and two collected, the notes would appear thus (*s*, 2), the letter *s* representing *several*. If in a half-mile of sandy roadway, a considerable number of specimens of *Spharagemon* were seen, but never close enough together to be abundant, the numbers would be indicated by the plus sign (+, 1). If a species was taken in a particular kind of habitat in nearly all stations of this habitat visited, or if it was regularly

[1] Facilities for determination were available at the biological station, and the species were identified as they were taken. With most of the species the writer had been acquainted, and the species soon became so familiar as to be recognizable at sight. In life there are many rather conspicuous peculiarities of color and of behavior which aid in recognition. Whenever there was doubt as to identity, as in the case of *Melanopli* particularly, specimens were caught and examined critically in the field, to avoid overlooking species of similar appearance. In all cases one or several specimens of each species were kept for verification. There is no reason why many familiar insects should not be recognized at sight as easily as birds are identified by ornithologists.

to be found in extensive areas representing this habitat, its frequency for that habitat was considered to be high. From the records which thus accumulated it was possible to arrive at a relative estimate of frequency and abundance for each species in its various habitats. Though the method is not free from error, it is the best which was available, and it is believed to be not far from a representation of actual conditions. Terms expressing degrees of frequency and abundance are *dominant*, *abundant*, *frequent*, *occasional*, *infrequent*, and *accidental*. These terms are used in the table of distribution on p. 153, and are there defined.

The Relation of the Animal to Plant and Animal Communities.

The Plant Association as an Index of the Habitat.—The area of the habitat as considered in this study has already been defined as the area conveniently marked by the extent of the plant association. In the plant association or plant community physical conditions and vegetation are generally uniform. In the early stages of development of vegetation, local physical conditions dominate. In later stages the vegetation assumes the type determined by climatic conditions, and exerts nearly complete control over local physical factors. Thus the grasshoppers in early stages of vegetation, as the *Œdipodinæ*, most of which live in very open grassland, are more intimately associated with physical conditions, which to them are more important, while those of advanced stages of vegetation depend more upon vegetational factors, and less upon the character of the soil. *Melanoplus islandicus*, associated with climax deciduous forest, is a species of the second type. The grasshoppers as a group are most abundant in early stages of vegetation in forest climates, while in grassland climates they occur abundantly in all stages. The plant association may thus be taken as the index of environmental conditions; it expresses the resultant of physical and vegetational conditions to which animals are subjected. Within the area of the plant association local variabilities in physical conditions are usually accompanied by local variabilities in the vegetation; the latter may exist independently. Grasshopper species are affected by these local differences.

Vertical Distribution.—The distribution of terrestrial animals in space is both vertical and horizontal (Shelford, '12*b*). Most of the grasshoppers of the Douglas Lake region belong to the ground and field (herbaceous) strata, as do the *Acridiidæ* in general. With the exception of the forest species which oviposit in wood, the eggs are laid in the soil. Most of the species require bare soil, and many of their activities take place directly upon the surface. *Stenobothrus* is more commonly seen upon the plants, and certain species of *Melanoplus* live upon the plants part of the time. *Podisma glacialis variegata* is a shrub-inhabiting species. Grasshoppers are in general typical animals of the ground stratum. Other families of *Orthoptera* are more typical of other strata.

Horizontal Distribution.—Within a region an animal species will select habitats or associations in which conditions of the optimum environment are most closely approximated. The table on p. 153 indicates that no two grasshopper species of the Douglas Lake region select the same set of environmental conditions. Certain of the species are similar in distribution, but none are identical. They replace one another in different habitats, with some overlap, and can be arranged in series according to gradients of environmental factors (Fig. 1, p. 156).

Although a single species may be found in more than one association, it is not equally abundant nor equally regular of occurrence in these associations. Certain of the grasshopper species are typical of only one association, as *Melanoplus fasciatus* in closed aspen forest. *Melanoplus atlanis*, the most generally distributed species, though abundant in five habitats, is most abundant in ruderal grassland, and very typical in such situations. Other grasshoppers are *more* characteristic of the other four associations in which *Melanoplus atlanis* is abundant.

The various habitats in which a particular species may be found happen to be more or less similar in physical and vegetational conditions. Data in the table on p. 153 indicate that those associations in which a grasshopper is found in common may agree only in containing certain or all of the conditions necessary for that species, and that there need be no successional or geographic relationships between the associations, nor is it a matter of concern whether the associations be native or ruderal, extensive or local.

The occurrence of a grasshopper species, or of several species, in two habitats or associations does not mean that these furnish similar environmental complexes for animals. It means simply that certain environmental conditions necessary for these particular species are *included* among the conditions provided by these habitats. Thus in the Douglas Lake region, *Melanoplus islandicus* is found in beech-maple forest and in the cedar-bog forest. These two associations are radically different in many respects, as habitats for animals. The entire range of conditions presented within the area of an association, particularly if it be extensive, is likely to be considerably more inclusive than the range of conditions required by many animal species. Taxonomic groups of animals which are affected more particularly by conditions *differing* in the two habitats, will be represented differently in them. It follows that very little reliance can be placed on comparisons of habitats on the basis of the study of a taxonomic group, such as grasshoppers, except in respect of the particular conditions critical to the species of this group. Comparisons of the entire animal communities of the two habitats would not be subject to this limitation, since nearly all of the environmental conditions within the two habitats would come into consideration.

Within any one association the animal species may be distributed generally throughout its area, as *Melanoplus angustipennis* in the bracken-blueberry growth; in certain instances it may be restricted to a part of the area characterized by a slight environmental difference; or it may occur in scattered parts of the association, characterized by scattered local differences, as *Scirtetica marmorata* in the lichen-covered patches within the bracken-blueberry growth.

The Animal Environment.—In addition to the physical and vegetational influences upon the animal species, that of its animal environment must also be recognized. Direct effects of the animal-environment upon the animal species are probably greater than the indirect effects produced by modification of physical and vegetational environments. Among these latter more general effects of the animal community are the accumulation of organic remains, and particularly the effects of phy-

tophagous animals upon vegetation. It is probable that animal environmental influences are greater than is commonly supposed, but that ordinarily they play a subordinate part as compared with physical and vegetational influences (cf. Shelford, '12*a*: 94).

The grasshopper species is not only affected by the animal environment, but is itself a part of it. So far as the relations of the grasshoppers to the association and with other species is concerned, about all that is known, in general, is that they are among the most important of the plant-eating animals of grassland associations, in which some of them are dominant species; and that they form the principal food supply for a comparatively large number of predaceous and parasitic enemies. It is not known to what extent different grasshopper species compete with one another. Differences in habitat and in time of activity may indicate removal of competition among certain species.

Successional Relations.

The successional relations of the Douglas Lake associations have been discussed by Gates ('13: 48), and a diagram illustrating the successions is included. The work on the grasshoppers has not covered so wide an area, consequently many of Gates' associations are not well represented. Fig. 1, on p. 156, will serve to illustrate successional relations of the associations in which grasshoppers were taken, and the changes in grasshopper species may also be seen, as one plant association is replaced by another. Initial stages in dry soil are shown at the lower left-hand part of the diagram; initial stages in wet habitats at the lower right. The two series converge at the top of the curve, in the climax beech-maple forest. The ordinary course of succession from marsh associations is toward bog forest; from beach grass into pine forest. These successions are not shown in the diagram. The aspen association is the result of secondary succession from pine forest, which is no longer well represented in the immediate region. Grassland associations between beach-grass and wet meadows are represented only by ruderal growths; which have originated mostly by secondary succession. Closed grassland is not represented, for invasion by forest occurs before it can develop.

Only the series leading from bare sand to climax forest through the aspen stages of burnt-over pine lands will be discussed in relation to grasshopper succession. The following table, taken from the distribution table on p. 153, and with the same notation, shows the grasshopper species of the various stages. Accidental and atypical occurrences are not recorded. It should be remembered that the bare soil habitat is never extensive in the region, and that grasshoppers of bare soil depend also upon nearby vegetation.

TABLE II.

	Bare Sand.	Beach-Grass.	Bracken-Blueberry.	Closed Aspens.	Beech-Maple.
Dissosteira carolina	Freq.[1]	Freq.	Occas.		
Spharagemon bolli	Freq.[1]	Occas.	Occas.		
Circotettix verruculatus	Freq.	Occas.	Occas.		
Arphia pseudonietana	Freq.[1]	Infreq.	Infreq.		
Hippiscus tuberculatus	Freq.	Infreq.	Infreq.		
Camnula pellucida	Freq.[1]	Freq.[1]	Freq.[1]		
Melanoplus angustipennis	Occas.	Freq.	Dom.		
Melanoplus luridus	.....	.....	Occas.		
Scirtetica marmorata	.....	.....	Infreq.[2]		
Melanoplus fasciatus	.....	.....	Infreq.	Freq.[1]	
Chloealtis conspersa	.....	.....	?	Infreq.	
Podisma g. variegata	.....	.....	.....	.....	?
Melanoplus islandicus	.....	.....	.....	.....	Freq.
Melanoplus atlanis	Freq.[1]	Abund.	Freq.	?	Infreq.

From examination of the table we see that there is a successive change of species with development of vegetation, and that even when species are not replaced with changes in associations, their numbers are successively increased or decreased.

The succession from bare sand to closed hardwood forest includes two successional series, the development from very open grassland growth to closed grassland, and the development of closed forest from open forest growth. The transition stage is the open aspen forest, in which trees are small and scattered. Ground conditions, dominated by the bracken-blueberry cover, are those of grassland which has not yet reached the closed stage. The change in ground conditions from those of grassland to those of closed forest is radical, as shown by the great difference

[1] Frequently found, usually not in numbers, but in a few places approaching abundance.

[2] More typical of scattered patches of lichen-covered surface; distribution in bracken-blueberry not continuous.

between the grasshoppers of the bracken-blueberry and closed aspen stages. Climax beech-maple conditions have probably not yet been fully developed, in the immediate region, from the closed aspens of the pine lands. The beech-maple forest of the morainic areas of the region represent the ultimate condition of present closed aspen areas.

The grasshoppers of the table show certain likenesses and differences in habitat-selection which may be correlated with their behavior characters. The first five species, all typical of very open situations, are active, motile forms, of strong and sustained flight, and are usually seen resting upon bare soil. They lay eggs usually in soil of loose texture. They are frequently seen on roads, and patches of bare soil, in the Douglas Lake region, and are abundant near the beach. They are frequently seen in the interstices between plants in open grassland, and become successively less numerous with the closing of the vegetation.

Camnula pellucida is less like the typical bare-ground *Œdipodinæ* in behavior. It is more variable in distribution, and though practically restricted to grassland, is more numerous in ruderal growths.

Melanoplus angustipennis is an interstitial species, and increases in abundance with the closing of the vegetation until the sand is relatively stable, with the admixture of a little humus, though the soil is still loose in texture.

Melanoplus luridus and *Scirtetica marmorata* have not been found in sufficient numbers to determine their status with satisfaction. The former appears to be a species of nearly closed grassland; the latter is more or less closely associated, in this region at least, with lichen surfaces that had not developed in earlier stages of herbaceous growth.

Melanoplus fasciatus and *Chloealtis conspersa*, in this and other regions, are associated with dry open forests and forest borders. They are more frequently short-winged, and exhibit a departure from grassland behavior. The latter is known to deposit eggs in wood.

Melanoplus islandicus is a shade-dwelling species of deep woods. It is flightless, and probably lays eggs in wood. *Podisma*

glacialis variegata has not been taken in the beech-maple forest, but probably occurs there. It differs from the other grasshoppers of the region in being of the shrub stratum, rather than of the ground or herbaceous strata.

The species in the table are arranged approximately in the order of succession of the associations in which they occur. *Melanoplus atlanis*, being more generally distributed, can hardly be assigned to a particular place in the series, and is placed at the bottom accordingly. It is most abundant in ruderal grassland, and is not at all common in forest.

A parallel development of vegetation in sand is seen in a region in central Illinois. The herbaceous vegetation is sand prairie, is very open in the initial stages, and is replaced by xerophytic oak forest before a closed grassland is reached. The habitat-relations of the various grasshopper species are discussed by Hart ('07). A number of the species of the Douglas Lake region are here represented in habitats occupying equivalent stages in the successional series.

The initial stages of herbaceous growth, characterized by a large proportion of bare surface, are accompanied by active, very motile grasshoppers which rest normally on the surface and which lay eggs in soil of loose texture. With the closing of the herbaceous growth grasshoppers of this habit gradually decrease in numbers, giving way to species which rest part of the time upon the vegetation, which are less motile, and which lay eggs in the less sterile types of soil of such situations. In sand regions of the forest climate, usually, forest invasion occurs before the herbaceous growth becomes closed. The ground conditions remain those of grassland until the forest approaches the closed stage, when the grasshoppers of open grassland are abruptly replaced by forest grasshoppers, which are less motile, usually flightless. They are fewer in species and individuals than grassland members of the group, in part because of the fact that in advanced forest stages, in which the ground is almost entirely covered with dead leaves, the soil is generally inaccessible for egg-laying, and oviposition takes place typically in wood.

Geographic Relations.

The vegetation of the region, as has already been mentioned, is composed of two geographic elements, that of the Northeastern Conifer Province and that of the Eastern Deciduous Province. In addition there are certain associations, chiefly made up of plants which cannot be assigned to these vegetation regions. Comparison was made of the geographic distribution of grasshoppers with that of the vegetation, and with their own local distribution.

Most of the species are generally northern in distribution. Of these *Podisma glacialis variegata*, *Melanoplus islandicus*, and *Chloealtis conspersa* may be assigned to the Northeastern Province. *Circotettix verruculatus*, *Melanoplus fasciatus*, *M. luridus*, *M. minor*, *Camnula pellucida*, and *Stenobothrus curtipennis* range in both northeastern and northwestern coniferous regions, extending south to varying distances in both Appalachian and Rocky Mountains. *Arphia pseudonietana* does not range so far to the east as these preceding species. *Arphia*, *Melanoplus luridus*, *M. minor*, *Camnula*, and *Stenobothrus* occur also throughout the northern part of the Prairie Province.

Spharagemon bolli and *Scirtetica marmorata* may be assigned to the Eastern Deciduous Province. *Hippiscus tuberculatus* is found in the northern parts of both prairie and deciduous forest. *Melanoplus angustipennis* is a prairie species, being found abundantly in sandy parts of the Prairie Province, ranging also west into the sage-brush country, in Utah.

Dissosteira carolina, *Melanoplus atlanis*, *M. femur-rubrum*, *M. differentialis*, and *M. bivittatus* are of very wide geographic distribution, ranging over most of the United States and much of Canada.

Certain species of the first group are rather sharply restricted to the coniferous forest regions, while others range well into the prairie and deciduous forest regions. *Chloealtis* and *M. fasciatus* range also into deciduous forest. *M. luridus*, *M. minor*, *Camnula* (in the northern prairie states), and *Arphia* range also into the prairie region. An excellent instance of the sometimes sharp boundary between two provinces is shown along the foothills of the eastern Rocky Mountains in Colorado. Here *Chloealtis*,

Circotettix, *M. fasciatus*, and *Camnula* are not found outside of the mountains, while *Arphia*, *M. luridus*, and *M. minor* are found on the plains. *Stenobothrus* bears no particular relation to climatic vegetation regions, as its presence is determined by local conditions of moisture.

The occurrence of *Melanoplus angustipennis* at Douglas Lake, so far from the prairie region, seems at first very unusual. So far as the writer is aware, the species is not recorded from Michigan, though it must occur all along the Lake Michigan shore, and is known from Ontario. Its most necessary environmental condition is sandy soil, and this is well developed along most of the shore-line of the Great Lakes.

The five species of most wide distribution geographically are those which have least definite habitat-preferences within a particular area. The extensive range, and the fact that these particular species are among those most important economically, as destructive to crops, is to be explained in terms of tolerance of widely varying conditions.

The species which are restricted to forest habitats in the Douglas Lake district are restricted geographically to forest provinces. Certain of the species found in grassland or in open forest in the region studied range outside the forest provinces, being thus clearly independent of forest growth, while others appear to be restricted to forested regions, though found in open habitats. It is probable that *Camnula pellucida* and *Circotettix verruculatus* are restricted to the mountain areas of Colorado by radical changes in physical conditions from mountains to plains, rather than by changes in vegetation.

In general, it may be said that grasshopper species associated with the climatic plant association have the same geographic range as this association. This range, when shared by many species, determines the ecological province. Where two similar climatic vegetation regions adjoin, as in the case of northeastern and northwestern conifer regions, the same grasshopper species may range over both, in similar associations. Certain species may also range locally into other provinces, in habitats locally approximating those of their own climatic association. Species associated with local habitats may be restricted to the province,

but more usually range over much wider areas (Shelford, '11: 606). Species of very general local distribution within a restricted area are likely to be very generally and very widely distributed geographically, and are the species which most frequently invade ruderal and cultural growths, and which tend to replace other species with the spread of civilization. Species of closed associations show more evident local and geographic relation to the vegetation than species of open associations, in which *local* physical conditions dominate (cf. Shelford, '12*a*: 89, 90).

Seasonal Relations.

Distribution of animals in space is more or less affected by distribution of animals in time. In dealing with the latter it seems that seasonal relations and life-histories of animals are comparable to habitat relations and habitat-preferences, when dealing with distribution in space.

The growing season is not uniform in physical and vegetational features of the environment. Seasonal changes are conveniently marked by changes in *aspect* of the vegetation. The successive changes in the environment for grasshoppers in the course of a season are somewhat different in forest associations from those in grassland.

A field of study of seven weeks is not long enough to determine seasonal relations of grasshoppers, nor to determine what species of grasshoppers occur in that region. *Chortophaga viridifasciata* (De Geer), an early spring grasshopper almost certainly occurs at Douglas Lake. *Melanoplus scudderi* (Uhler) and *Melanoplus punctulatus* (Uhler) may reasonably be expected to occur within the region. Both are short-winged forest-inhabiting species of late summer and autumn.

The time of adult activity of such species as were found, however, is known; the species may be arranged according to life-history into the following groups:

1. Species which hibernate as nymphs, appearing as adults in spring, remaining active only during early summer, represented by *Hippiscus tuberculatus*.
2. Species which hibernate as eggs, maturing very early in summer or late in spring, becoming scarce or disappearing by about September 1. *Melanoplus minor*, *M. bivittatus* (sometimes persisting in numbers till frost), *M. fasciatus* (this species may more properly belong in the fourth group).

3. Species which mature in spring or early summer, but which remain abundant until frost. *Chlœaltis conspersa, Melanoplus angustipennis, M. atlanis, M. femur-rubrum.* The last two are known to be two-brooded, and *M. angustipennis* probably is also, in parts of its range.
4. Species which mature in early July, remaining active until frosts. This is the common grasshopper life-history. *Stenobothrus curtipennis, Camnula pellucida, Dissosteira carolina, Spharagemon bolli, Scirtetica marmorata, Circotettix verruculatus, Melanoplus islandicus, M. luridus.*
5. Late-maturing species, appearing from late in July to the middle of August, and remaining until frosts. *Arphia pseudonietana, Podisma glacialis variegata, M. differentialis.*

The different timing of the period of activity of the species may be correlated with one or both of two kinds of seasonal difference in environmental influence: (1) Changes in physical and vegetational conditions necessary for the various activities. Conditions of temperature, moisture, vegetation, etc., change so materially with the season as to present very different environments for animals at different times of the year. Grasshoppers of different habitat-preferences may perhaps occupy the same area at different seasons. Life-histories are affected by geographic variation of climatic conditions. The entire complex of behavior characters of the animal is intimately associated with its life-history (Shelford, '12*b*: 334). (2) Seasonal differences in antagonistic influence of other animals, particularly those of similar requirements. These influences among animals which eat the roots of the corn plant and the strawberry plant are discussed by Forbes ('09: 296). Different species of certain insect genera, among them *Arphia* and *Hippiscus*, which are of similar habits and which occur in the same association, sometimes are active during successive parts of the season. One species of a genus may be completely replaced by another in a very short time, the second species continuing abundantly during the remainder of the season (Vestal, '13*b*). This replacement of one insect by another of similar habits is not uncommon among species of one genus, though not confined within genera. The differences in time of appearance among all the grasshopper species within a region, with the result that within some of the associations fewer species occur together at one time, may perhaps be accounted for partly in terms of antagonistic animal influence. The fact that grasshopper species of unique habits, which occupy

certain habitats by themselves, so far as grasshoppers are concerned, have the most common type of life-history, hibernating in the egg stage and active from early July till frosts, suggests that antagonistic influence is not a factor in determining *their* life-histories. Such species are *Stenobothrus curtipennis* in marshy growths, and *Melanoplus islandicus* in deep forests.

It appears that the species with least definite habitat-preferences (*Melanoplus atlanis*, *M. femur-rubrum*, *M. bivittatus*) have also least definite life-histories. They mature early, remain active till frosts, and are sometimes two-brooded. Their wide distribution in time is probably due to the same cause as their wide distribution in space, namely, their lack of responsiveness to slight differences in environmental conditions.

V. Summary.

Distribution of grasshopper species within the region studied bears evident relation to the plant associations. The plant association is the index to environmental conditions, and its extent marks the area of the habitat. In studies of local distribution within a region, all the plant associations, including local and ruderal associations, should be considered, since otherwise certain habitat relations may be overlooked.

As an environmental complex, the plant association is usually more inclusive than the total of conditions required by a particular species, particularly if it is climatic or extensive. Associations may be similar as environments for grasshopper species if they agree merely in including physical and vegetational conditions critical to those species. Grasshoppers select habitats or associations in which favorable conditions are to be found, irrespective of past history, extensiveness, geographic or successional relationships of the vegetation. There is very seldom any direct relation between grasshopper species and species composition of the plant associations, as few grasshoppers are selective feeders.

Most of the grasshopper species are of the ground stratum, and soil conditions are essential. These grasshoppers are typical of open herbaceous associations, characteristic in initial stages of vegetational development in dry ground. Species of open forest

are mostly grassland forms, since ground conditions are essentially the same in both situations. In closed forest and moist herbaceous associations species and individuals are less numerous, are not confined to the ground stratum, and are more intimately associated with vegetational conditions. Grasshopper species can be arranged according to gradients of environmental factors (Fig. 1, p. 156).

Grasshopper succession is incidental to the development of vegetation. The change is not only one of species, but of habits as well.

Grasshopper species have in general the geographic range of the types of associations which include the necessary physical and vegetational conditions. The ranges of many species are in agreement with the areas of vegetation provinces. Species of least definite local distribution are widespread geographically.

Seasonal differences in time of activity of grasshopper species are marked. This is probably partly due to antagonistic influence of other animals. Seasonal and local distribution are interrelated. Species of indefinite local distribution have also least definite time distribution.

UNIVERSITY OF COLORADO.

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THE ASEXUAL CYCLE OF PLANARIA VELATA IN RELATION TO SENESCENCE AND REJUVENESCENCE.

C. M. CHILD.

I. The Life Cycle under Natural Conditions.

During early spring in the region about Chicago, a planarian appears in temporary ditches and pools, particularly in those which are more or less filled with dead leaves. It is also often found in permanent bodies of water such as springs, permanent ponds and brooks, but seems to attain the greatest numbers in the temporary ditches and pools. The animal is apparently the species recently described by Stringer ('09) and named *Planaria velata*. The shape and proportions of the larger individuals are indicated in Fig. 1.

When the animals first appear soon after the ice melts they are mostly only 2–3 mm. in length and commonly light in color. They grow rapidly and soon the dorsal surface becomes very deeply pigmented so that they appear almost black. They are very active and their locomotion is much more rapid than that of most other fresh water planarians. During this period they react readily to meat of various kinds and can be collected in large numbers by placing pieces of meat in the water. In about four weeks they attain a length of 12–15 mm., their movements gradually become slower, they cease to react to food, become light gray in color from loss of pigment and sooner or later the pharynx disintegrates.

Within a few days after these changes a process of division begins. As the worms creep about, the extreme posterior end adheres to the substratum and the rest of the animal pulls away and leaves it behind as a small fragment which becomes more or less spherical and within a few moments is covered with a slime which adheres to the underlying surface and hardens into a cyst. This process of division is repeated, often several times within a few moments, so that as the animal moves across the

containing vessel it may leave behind it a series of such pieces. The pieces vary considerably in size, some being as large as 1.5 mm. in diameter, some only about 0.5 mm. The process continues until half or two thirds or sometimes even more of the worm is separated into pieces and then the anterior region including the head may encyst without further division or in some cases dies.

I

Under natural conditions the encysted pieces remain quiescent during the summer and the following winter and in early spring emerge from the cysts as minute, very active worms which at once begin to feed and grow and repeat the cycle. As I have determined by experiment, the encysted pieces are not capable of withstanding desiccation and it is probable that this fact is connected with the occurrence of the worms in ditches and pools partly filled with dead leaves. In such localities even though the water disappears, the bottom under the thick layer of leaves is always more or less wet and the encysted pieces are not subjected to drying.

During the last thirteen years I have collected these worms almost every year and have never found a single individual with mature sexual organs or even any indication of sexual reproduction. Every year the active period ends with decrease in activity, cessation of feeding, loss of pigment, fragmentation and encystment of the fragments.

In this species then, under the conditions where it occurs in this locality, development and growth result in a process of senescence, the individual breaks up into fragments which undergo regulation within the cysts to small whole animals, and these are to all appearances physiologically as well as morphologically young and are capable of repeating the life cycle. In short, senescence is followed in these animals not by death but by asexual reproduction and rejuvenescence.

During a number of years I have kept a stock of these worms in the laboratory, have bred them through several asexual generations and have subjected them to various experimental conditions. The results of this asexual breeding and the experi-

mental modifications of the life cycle will be discussed in another paper.

II. The Physiological Resistance to Depressing Agents of Young and Old Worms.

In these experiments the method of comparing resistances which I have called the direct method was used. Here the depressing agent is used in sufficiently high concentration to kill the animals within a few hours and the occurrence of death is determined by disintegration of the worms which begins within a few moments after death. This method has been fully described in another paper (Child, '13*a*). In that paper it was shown that with this method the animals with the higher rate of metabolism or more strictly of cell respiration are less resistant and therefore die and disintegrate earlier than those with the lower rate. Thus the differences in resistance enable us to compare the rates of respiration and so in a general way the rates of metabolism.

In Table I. the first vertical column gives the length of time in the depressing agent in hours and minutes, the second the serial numbers of the lots of worms compared, and the columns I.–V. under "Stages of Disintegration" give the number of worms of each lot in each stage of disintegration at each time. As regards the five stages, I have found it convenient to distinguish more or less arbitrarily these stages in the process of disintegration, for disintegration usually appears first in certain definite regions of the body while other regions are still alive and show movement and it follows a more or less regular course (Child, '13*a*). The five stages are briefly characterized as follows:

I. Intact, no disintegration.

II. Disintegration beginning, usually in head region.

III. Body beginning to disintegrate but form still retained.

IV. Margins disintegrated, form disappearing in consequence of swelling of tissues and separation of cells.

V. All epithelium and pigment gone; swelling of tissues has extended to all parts and original form has disappeared.

The distinction of these stages makes it possible to compare

different lots of worms more closely than if only the time of complete disintegration were noted.

In Table I. Lot 1 consists of ten worms 1.5–2 mm. in length, which had emerged from cysts within three or four days preceding and had been fed once with pieces of earthworm after emergence. Lot 2 consists of ten worms 13–15 mm. which had been raised in the laboratory from cysts with earthworm as food and were almost ready to encyst again.

TABLE I.

Series 77. KCN 0.001 mol.

Length of Time in KCN.	Lots.	Stages of Disintegration.				
		I.	II.	III.	IV.	V.
1.30	1	8	1	1		
	2	10				
2.00	1	5	1		1	3
	2	10				
2.30	1	4	1			5
	2	10				
3.00	1	2	2	1		5
	2	10				
3.30	1			3		7
	2	6	3	1		
4.00	1					10
	2	3	5	1	1	
4.30	2		8	1		1
5.00	2		4	4	1	1
5.30	2		1	4	3	2
6.30	2				3	7
7.30						10

It is evident at once from the table that the resistance of the worms of Lot 1 recently emerged from cysts is very much less than that of the large worms of Lot 2. Disintegration begins in

Lot 1 after one and one half hours in KCN, while the worms of Lot 2 are still intact and slowly moving about. In Lot 2 disintegration begins after three hours. All the worms of Lot 1 are completely disintegrated after three and one half hours, those of Lot 2 after seven and one half hours, *i. e.*, the survival time of Lot 2 is nearly double that of Lot 1. In other words the worms of Lot 1 have a much higher rate of metabolism than those of Lot 2.

That the difference in size of the worms is not responsible for the difference in survival time is evident for two reasons: first in these flattened elongated animals the surface increases almost as rapidly as the volume and second the time of beginning of disintegration (Stage II.) is much later in Lot 2 than in Lot 1. The earliest stages of disintegration involve the external surface of the body and the surface of the large worms including the cilia remains alive for a much longer time than that of the small worms. Moreover, if the difference in size determined the difference in survival time we should expect that this would be much greater since the small worms are only a minute fraction of the size of the larger. The difference in the rate of the metabolic processes affected by the KCN is the only factor which will account for the results (Child, '13*a*).

Unfortunately it has thus far been impossible to compare the worms emerging from the cysts with young worms hatched from eggs because I have never observed sexual reproduction in this species, but the difference in rate of metabolism between the small and large worms is similar to the difference known to exist in other forms between young animals sexually produced and old.

It is, however, not necessary to use the extremes of the life cycle for comparison. Animals in various stages of growth may be compared and in all cases those which are nearer the stage when encystment occurs, *i. e.*, those which are older as regards growth and development, show the higher resistance.

In Table II. the survival times of a series consisting of five worms 5–6 mm. in length (Lot 1) and five worms 11–12 mm. (Lot 2) are given.

TABLE II.

Series 64, I., II. KCN 0.001 mol.

Length of Time in KCN.	Lots.	Stages of Disintegration.				
		I.	II.	III.	IV.	V.
2.30	1	2	3			
	2	5				
3.00	1		3	1	1	
	2	5				
3.30	1		1	2	1	1
	2	3	2			
4.00	1				1	4
	2	1	4			
4.30	1					5
	2		4	1		
5.30	2			5		
6.30	2				4	1
7.30	2					5

In this series also the younger worms show less resistance, which signifies a higher rate of metabolism, but a comparison of Table II. with Table I. shows that Lot 1 of Table II. has a longer survival time than Lot 1 of Table I., *i. e.*, worms of 5–6 mm. in length have a lower rate of metabolism than worms recently emerged from cysts. These facts show that a progressive decrease in the rate of metabolism occurs during the growth of the animals. Those newly emerged from cysts have the highest rate, those which are full-grown and nearly ready to fragment and encyst have the lowest rate, while intermediate stages show rates between these two extremes.

These results have been confirmed by various other series with both KCN and alcohol. The small newly emerged worms die much earlier in all cases than the large worms. The differences in resistance to KCN, alcohol, etc., between young and old animals are the same in animals freshly collected from their natural habitat as in animals bred for one or more generations in the laboratory.

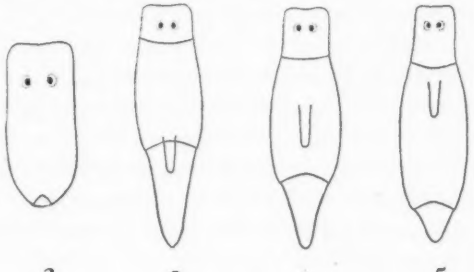
The results obtained in this way are further confirmed by the much greater activity of the small recently emerged animals. They move much more rapidly, are much more irritable and show a much higher rate of growth than the large animals. And finally the small worms from the cysts are capable, as noted in the preceding section, of repeating the life cycle. There can I think be no doubt that the worms emerging from the cysts are physiologically young and that they undergo a process of senescence as they grow in size. Evidently a process of rejuvenescence is associated in some way with the asexual reproduction which follows growth and development.

III. Experimental Reproduction.

1. *The Course of Experimental Reproduction.*

The process of reproduction of whole animals from pieces isolated by section is very similar to that in other planarians. Pieces from any region of the body and above a certain limit of size, which varies somewhat with the region, are capable of giving rise to whole animals.

As in other species of Planaria, the process consists in part of the outgrowth and differentiation of embryonic tissue from the cut surface and in part of redifferentiation of other tissues to a greater or less distance from the cut surface. In pieces of equal length the amount of anterior new tissue is greater and of posterior new tissue less in those from the anterior region of the body, while with increasing distance of the end of the piece from the head region the amount of anterior new tissue increases and



that of posterior new tissue decreases. The development of the new head is more rapid in anterior than in posterior pieces. The position of the new pharynx is posterior to the middle in anterior and anterior to the middle in posterior pieces. Short pieces from the extreme anterior region frequently fail to develop a new posterior end. Fig. 2 shows a piece of this kind. Figs. 3, 4 and 5 show three pieces, the first from the anterior, the second from the middle and the third from the posterior region. The different amounts of new tissue produced are seen in the figures. All these graded differences, like those in *Planaria dorotocephala* (Child, '11*c*), indicate the existence of a physiological gradient of some sort along the axis. As a matter of fact this gradient is essentially similar to that which exists in *P. dorotocephala* (Child, '12, '13*c*).

2. *The Encystment of Artificially Isolated Pieces in Relation to Size of Piece and Region of Body.*

Pieces isolated by section may undergo the regulation to whole animals either with or without encystment. The frequency of encystment varies with region of the body from which the piece is taken, with the size of the piece and with the physiological age of the animal. The following records of series will serve to illustrate this. In these series a number of worms, ten, twenty or twenty-five, from the same stock and as nearly as possible of the same size and in the same physiological condition are cut into a number of as nearly as possible equal pieces, the corresponding pieces are placed together in one lot and results recorded for each piece. Since different numbers of worms are used in different series the results are given in percentages.

Series 19, April 13, 1911.—Ten worms, full grown (12–14 mm.), but still feeding and deeply pigmented. Heads removed and remainder of body cut into two equal pieces, *a*, the anterior, and *b*, the posterior. Table III. shows the percentages of the pieces which develop into whole worms without encystment and of pieces which encyst soon after the operation and emerge, from a few days to several weeks later, as whole worms after regulation in the cysts.

TABLE III.

	No Encystment.	Encystment.
a	90	10
b	60	40

Series 20, April 13, 1911.—Ten worms from same stock, of same size and in same condition as Series 19. Heads removed and body cut into four equal pieces, *a*, *b*, *c*, *d*, *a* being the most anterior. Table IV. gives the results.

TABLE IV.

	No Encystment.	Encystment.
a	90	10
b	80	20
c	30	70
d	20	80

Series 27, April 17, 1911.—Ten worms like those of Series 19 and 20 in size and condition. Heads removed and body cut into eight equal pieces, *a*–*h*, *a* being the most anterior. The results are given in Table V.

TABLE V.

	No Encystment.	Encystment.
a	20	70
b	10	90
c		100
d		100
e		100
f		100
g		100
h		100

It is evident from these three series and abundantly confirmed by numerous others, first, that the frequency of encystment of pieces increases from the anterior to the posterior end of the body and second, that the frequency of encystment increases as the size of the piece decreases. In all these series the greater frequency of encystment in more posterior pieces is evident in greater or less degree. In Series 19 where the pieces represent halves of the body the percentages of encystments are small, in Series 20, composed of $\frac{1}{4}$ pieces, they are larger except in the

most anterior piece and much larger in the two posterior pieces *c* and *d* which together equal *b* of Series 19. And finally, in Series 27 which consists of $\frac{1}{8}$ pieces all the pieces encyst except 30 per cent. of *a* and 10 per cent. of *b*. When the pieces are cut still smaller all encyst.

The frequency of encystment then shows in pieces of equal size a gradation from the anterior to the posterior end of the body and indicates the existence of some sort of a physiological gradient in the animal. Encystment may, however, occur in pieces from any region if they are sufficiently small, but in general anterior pieces must be smaller than posterior pieces to give the same frequency of encystment. This fact indicates that the physiological state of the piece differs in some way with its size. As a matter of fact this species possesses essentially the same sort of gradient in rate of metabolism as *Planaria dorotocephala* (Child, '13*a*, '13*c*) and the relation between frequency of encystment, region of the body and size of the piece depends upon the existence of this gradient and the changes in rate of metabolism which occur in pieces from different regions of the body and of different size after isolation. Further consideration of these points is postponed to another time.

3. *The Frequency of Encystment of Pieces in Relation to Temperature.*

Series 53, October 5, 1911.—Animals 9–10 mm. in length were selected from a stock which had been kept at a temperature of 20° C., the heads removed and the bodies cut into four equal pieces *a–d*. Lots of ten each of each of the four pieces were placed in three different temperatures, 10°, 20° and 28–30° C. Table VI. gives the results in percentages.

It is evident at once from Table VI. that the frequency of encystment is greater with higher than with lower temperature, *i. e.*, the higher the rate of metabolism in the pieces the greater the frequency of encystment. Numerous other series give the same results without exception, not only for pieces, but for whole worms. Worms which have been kept at a temperature of 20°, when placed in a temperature of 30° will often encyst entire while at 20° they remain active until they fragment and the pieces encyst, and at 10° many of them do not encyst at all.

TABLE VI.

Temperature.	Pieces.	No Encystment.	Encystment.	Dead.
10°	*a*	100		
	b	90	10	
	c	20	80	
	d	10	90	
20°	*a*	100		
	b	70	30	
	c		100	
	d		100	
28–30°	*a*		100	
	b		100	
	c		100	
	d		100	

4. *The Frequency of Encystment in Pieces in Relation to Age.*

In the very small young worms recently emerged from cysts pieces, unless very small, usually reproduce whole worms without going through a period of encystment. As the worms increase in size and become physiologically older the frequency of encystment increases until in worms which are almost ready to fragment and encyst naturally all pieces resulting from section usually encyst.

The differences in this respect between half grown worms, worms which are about full grown but have not yet ceased to feed and still retain their dark color and worms which have stopped feeding and become gray in color are shown in the three series following.

Series 47, September 21, 1911.—Twenty worms about half grown (7 mm. in length) were cut into four equal pieces, *a–d*. The percentages of regulation without encystment and of encystments appear in Table VII.

TABLE VII.

	No Encystment.	Encystment.	Dead.
a	95		5
b	95	5	
c	55	45	
d	20	80	

Series 56 I, October 12, 1911.—Ten worms full grown but still dark in color and still feeding. Body cut into four equal pieces, *a–d*. Table VIII. gives percentages of encystments.

TABLE VIII.

	No Encystment.	Encystment.
a	60	40
b		100
c		100
d		100

Series 58 I, October 13, 1911.—Ten worms, full grown, gray in color and no longer feeding. Body cut in four equal pieces, *a–d*. Table IX. gives percentages.

TABLE IX.

	No Encystment.	Encystment.
a		100
b		100
c		100
d		100

The older worms show the greater frequency of encystment of pieces. The same results have been obtained in other similar series without exception.

5. *The Physiological Condition of Animals Reproduced from Artificially Isolated Pieces.*

The animals reproduced from pieces isolated by section are physiologically young, whether a period of encystment occurs or not. In this respect they are similar to the worms produced from the pieces which separate and encyst naturally. Small pieces cut from the bodies of old worms and allowed to reproduce whole animals show the same differences in rate of metabolism from old animals as the worms emerging from cysts naturally produced. The differences in susceptibility to cyanide are essentially the same as in Table I. Moreover, these small worms arising from pieces of large old worms are capable of rapid growth if fed and of repeating the life cycle. As they grow the rate of metabolism, as indicated by their susceptibility to

cyanide, decreases, the rate of growth and the degree of activity also decrease, they finally stop feeding, lose their dark color and give rise to cysts again and from these a new generation of young worms emerges. Stocks of animals produced from pieces have passed through this cycle repeatedly in the laboratory.

The degree of rejuvenescence in this experimental reproduction varies with the size of the piece. The smaller the piece, the more extensive the reorganization and the younger the worm which results. In all respects these results are essentially the same as those obtained with *Planaria dorotocephala* and described in an earlier paper (Child, '11*b*).

It is evident also that there is no essential difference in this respect between the process of fragmentation in old worms and the reproduction of young worms from the encysted pieces in nature and the process of experimental reproduction of animals from pieces isolated by section. In nature the fragmentation occurs only in old animals by a process characteristic of a certain stage of the life cycle. In experiment the pieces can be isolated at any stage of the life history and may be of any size. In both cases the reorganization, together with the period of starvation which is also a factor as will appear, brings about rejuvenescence and the worms thus produced are capable of repeating the life history from the stage at which they begin again to feed to the stage of fragmentation.

IV. The Nature of the Process of Encystment.

It has been shown that the frequency of encystment of pieces increases with rising temperature, with decreasing size of the piece, with increasing distance of the level of the piece from the head region and with advancing age of the animals. Pieces from any region of the body may encyst if the temperature is sufficiently high, if the pieces are sufficiently small or if the animal is sufficiently old. All of these conditions must have something in common as regards their effect upon the pieces since all produce similar results. What is this common factor?

When a piece is cut from the body it is stimulated and its rate of metabolism increases. This is generally admitted but it can also be demonstrated by the cyanide method. The suscepti-

bility to cyanide of a piece immediately after isolation is much greater than that of the corresponding region of the body in an uninjured animal of the same age and physiological condition. This greater susceptibility of the piece means that it has been stimulated by the act of isolation. After this sudden rise its susceptibility to cyanide decreases gradually during twenty-four hours or more and in small pieces may fall below that of corresponding regions in the uninjured animal (Child, '13*b*). This decreasing susceptibility means that the rate of metabolism in the piece is gradually decreasing as the stimulation resulting from section gradually disappears.

The cyanide method shows further that the degree of stimulation increases as the size of the piece isolated decreases and also as the distance of the level of the piece from the head region increases. In other words smaller or more posterior pieces are more stimulated by the act of section than larger or more anterior pieces. And finally pieces cut from worms at a higher temperature within certain limits are more stimulated and show a greater increase in rate than pieces from worms at a lower temperature.

These relations between the degree of stimulation of pieces and the factors of size of piece and region of the body and various external conditions have been worked out completely for *Planaria dorotocephala* and the data will be presented in full elsewhere. Sufficient work has been done on *P. velata* to show that the relations are essentially the same as in *P. dorotocephala*, but since the work on the latter species furnishes the foundations for the conclusions and since the data for that species are in more complete form and will be published in a short time the evidence for the above statements concerning the degree of stimulation in pieces of *P. velata* is not presented in detail.

So far then as region of the body, size of piece and temperature are concerned the frequency of encystment of pieces in *P. velata* runs parallel to the degree of stimulation by the act of section. Apparently the more the piece is stimulated by section the more likely it is to encyst.

The process of encystment in this species consists in the rapid secretion over the surface of the body of a thick slime which

soon hardens into a tough membrane and forms the cyst. It is a familiar fact that stimulation is often followed in the turbellaria by the secretion of a large amount of slime. That is exactly what occurs in these pieces and in this species the slime hardens and forms the cyst. Apparently then the encystment of pieces in *Planaria velata* is simply the result of a sudden stimulation. Any factor that increases the stimulation increases the frequency of encystment.

As regards the greater frequency of encystment with advancing age of the worms, I have not been able to reach a definite conclusion based on experiment, but my observations indicate that old worms secrete more slime on stimulation than young. Apparently the gland cells either increase in number or the quantity of the substance in them which produces the slime increases as the animals grow older.

When the slime which produces the cyst first appears it is soft and an active whole animal is able to creep out of it without difficulty, but the pieces are much less active and do not succeed in escaping from it before it hardens. If the cysts are carefully opened with needles soon after they are formed and the pieces removed without injury or any great degree of stimulation they usually do not encyst again but develop into whole worms while free. But if they are injured or otherwise strongly stimulated they commonly encyst a second time.

In short all the facts indicate that encystment of pieces is merely a result of the stimulation accompanying section. It is not an adaptation to conditions or a preparation for the future in any sense. The animals do not encyst because they usually live in temporary bodies of water but they are able to live under these conditions because they encyst.

V. The Process of Fragmentation in Old Worms.

The process of fragmentation in nature is very evidently similar in character to the process of zooid-formation and fission in *Planaria dorotocephala* and *P. maculata* (Child, '11*e*). In consequence of increase in length of the body and the decrease in rate of metabolism as the animal becomes older the posterior regions of the body usually become to some extent physio-

logically isolated from the dominant region (Child, '11*a*, '11*d*).

That the occurrence of fragmentation is connected with a decrease in the rate of metabolism and consequent physiological isolatiion of posterior regions is clearly indicated by the fact that fragmentation may often be induced, even in worms which are not full-grown, by suddenly lowering the temperature ten to fiftcen degrees. In such cases fragmentation usually begins in the posterior region within a few days.

The degree of isolation is not sufficient to permit development at once into a new individual but it is sufficient to permit some degree of independence in motor reaction, consequently, at some time when the worm is creeping the posterior end attaches itself and the rest of the body pulls away from it, as in *P. dorotocephala*. Apparently the greater part of the body in old fragmenting animals consists of a series of these small zooids for in most animals fragmentation continues until only the anterior third or fourth of the body together with the head remains. This anterior piece may then encyst or may undergo rejuvenescence without encystment and after some weeks give rise to a new posterior end, or in some cases it dies.

The posterior zooids are present only dynamically and not morphologically, at least not visibly, and they are not to be thought of as absolutely fixed stable entities. When the animal is strongly stimulated it is able to control the whole length of the body and for the time being the posterior zooids may almost or quite cease to exist, only to reappear after the stimulation is over. When such zooids are established the regions at their ends must be subjected to constantly varying correlative conditions. Sometimes they may form a physiological posterior part of one zooid, at other times an anterior part of another and at still others a part of neither. Such changes in correlative conditions must tend to weaken and eliminate the existing structure in those regions since the development of such structure depends on a certain degree of constancy in correlative factors. In this way zones of structural weakness arise and these are the zones where separation occurs.

Occasionally, either in consequence of weakness or perhaps because the physiological isolation of the posterior regions is

insufficient the worm fails to fragment. In such cases parts of the body may become greatly elongated and a string of connected masses may arise. Figure 6 shows such a case. In the posterior region four distinct masses can be distinguished. These are connected by slender bands which are merely portions of the body greatly reduced in diameter. These four masses are connected with the anterior portion of the body by a long slender band resulting from the stretching of the middle region in consequence of the attempts of the head region to pull away from the attached posterior parts. These greatly elongated regions of the body consist of little more than the body-wall and muscles; the alimentary tract and the parenchyma may be almost or entirely squeezed out of them. This animal finally became surrounded by a cyst in the form shown in the figure, but later the connecting strands apparently atrophied, the pieces became entirely separate and each produced a whole worm.

6

VI. The Development of the Whole Animal Within the Cyst.

The development of the animal from the encysted piece, whether isolated artificially by section or by the natural process of fragmentation, is similar in all respects to the regulatory development of pieces which reproduce new wholes without encystment. This is shown to be the case by the removal of the cysts from pieces at various stages of the process. In all cases the pieces are simply undergoing regulation. The process within the cyst may, however, be slower than in the unencysted piece, probably because the supply of oxygen within the cysts is less than in the water.

The natural method of asexual reproduction in this species does not then differ essentially in any way from the process of experimental reproduction. The process of fragmentation gives

rise to the same conditions in the piece as experimental isolation by section and the further history is the same in both cases.

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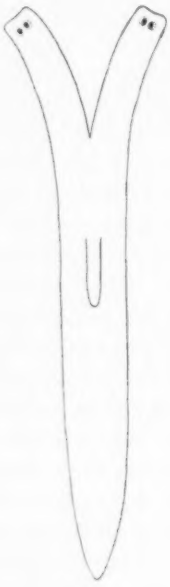

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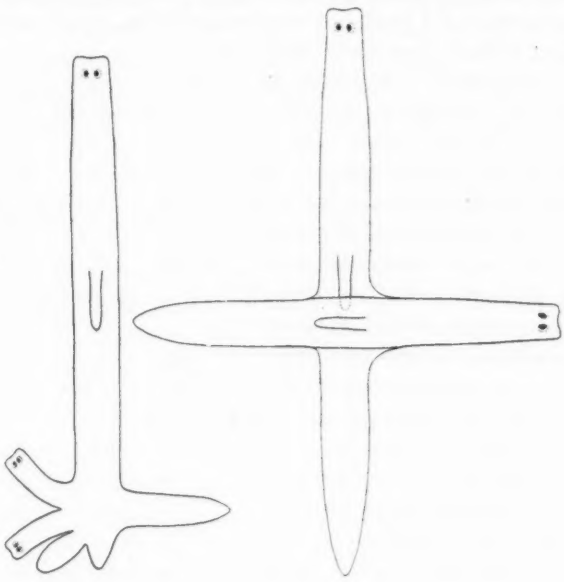
Many teratological forms result from irregularities in fragmentation or incomplete separation. The most common are partial duplications of anterior or posterior regions (Figs. 7 and 8) but various other forms appear. In Fig. 9, for example, a case is shown in which an incompletely separated posterior piece gave rise without encystment to two heads, a tail and two outgrowths of uncertain character, and Fig. 10 shows a case in which two worms with axes at right angles to each other are united by the middle regions of their dorsal surfaces. Ordinarily the larger animal carried the other about on its back as in the figure, the ventral surface of the smaller worm being uppermost. Fig. 11 represents a case of so-called axial heteromorphosis and in Fig. 12 two heads appear at the posterior end of the larger individual and dorsal to them a tail. Evidently new

polarities arise very readily in the small pieces which result from fragmentation, probably because the pieces are so short that the



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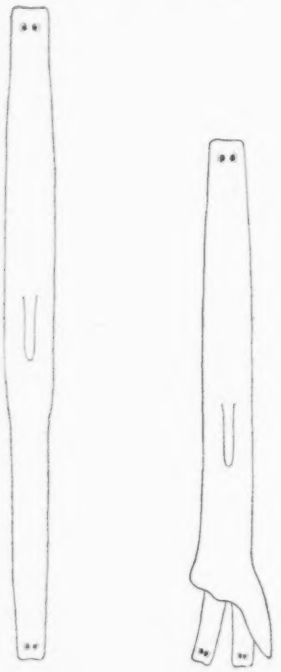
original axial gradient (Child, '13*c*) is practically eliminated and chance differences in the rate of metabolism in different parts of the piece are sufficient to establish new polarities.

VII. Conclusion.

In *Planaria velata* the individual very evidently undergoes a process of senescence as it grows and either experimental or natural asexual reproduction brings about rejuvenescence. Moreover, the animal apparently returns to essentially the same physiological stage with each generation, for the species is able to persist without sexual reproduction and, as a following paper will show, numerous asexual generations have been bred in the laboratory without any indication of senescence of the stock.

I have shown elsewhere (Child, '11*b*) that the regulation of

isolated pieces of *Planaria dorotocephala* brings about rejuvenescence to a greater or less extent, according to the size of the piece, the smaller piece giving rise to an animal which is physiologically younger than that produced by a larger piece. In that species starvation may also be a factor in rejuvenescence. Some experiments on the effect of starvation on *Planaria velata* will be described in another paper. At present it need only be said that the result is the same in both species.



11 *12*

In my earlier paper on senescence the conclusion was reached that senescence results from the accumulation of structural products of metabolism which constitute in one way or another obstacles to the chemical reactions. The processes of differentiation and growth undoubtedly operate also in another way not considered in the earlier paper, to bring about a decrease in the rate of metabolism per unit of weight or volume. What we are accustomed to call the undifferentiated or embryonic cell represents the general metabolic substratum of the organism. Differentiation consists in the formation and accumulation of certain substances in the cell, some of which constitute more or less permanent structural features. At least certain of the substances composing these structural features are relatively stable under the usual physiological conditions and while certain chemical changes may occur in them, they are not broken down and eliminated to so great an extent as certain other substances. This relative stability must, in fact, be the basis of their persistence as elements of structure. The accumulation of these structural

substances within the cell brings about a decrease in the general metabolic activity per unit of weight or volume because it decreases the proportion of the material involved in the general metabolic reactions to the inactive or less active material. The decrease in the proportion of the general metabolic substratum characteristic of the embryonic cell constitutes to some extent a histological criterion of the physiological change in the cell.

In short, the decrease in rate of metabolism per unit of substance, which is characteristic of development and senescence, is undoubtedly due in part to the fact that the proportion of the cell substance concerned in the general metabolic activity is decreasing and the proportion of less active or relatively stable substance is increasing. Changes in the size of the cell or in the size relations of nucleus and cytoplasm (Minot, '08) are not necessary factors in the result.

To what extent the decrease in the rate of metabolism during senescence is due in a given case to actual decrease in the rate of chemical reaction and how far to a decrease in the proportional amount of chemically active or more active substance is often difficult to determine, but it is probable that in some cases, or even in some cells of the individual, the one factor and in others the other is the more important.

As regards *Planaria velata*, the facts are that the rate of metabolism decreases during growth and development and increases when the substances previously accumulated are removed, either by regulatory reorganization, or by starvation. These facts show very clearly that in one way or another the accumulation of material in development decreases the rate of metabolism and its removal brings about an increase in rate. Senescence and rejuvenescence in this species consist essentially, I believe, in these changes.

Summary.

1. After a period of growth and activity *Planaria velata* undergoes fragmentation from the posterior end forward, the fragments encyst and give rise by a process of regulation to whole worms of small size.

2. During the period of growth the worms are undergoing senescence, as the decrease in rate of metabolism indicates, but the small worms which emerge from the cysts are physiologically, as well as morphologically young, possess a high rate of metabolism and are capable of repeating the life cycle.

3. In pieces isolated by section the frequency of encystment increases as the level of the piece becomes more posterior in the body, with decreasing size of the piece, with rising temperature and with increasing age of the animal. The facts indicate that encystment is the result of stimulation. The stimulation may result from section, from fragmentation, from a rise in temperature or from other conditions.

4. The development of the encysted piece into a new whole animal is essentially the same process as the regulatory development of unencysted pieces.

5. This species is able to live for an indefinite number of generations without sexual reproduction. Each new asexual generation represents a return to essentially the same physiological and morphological stage. In other words, senescence leads to reproduction and the process of rejuvenescence in each asexual cycle carries the organism back to the same stage of youth.

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DEVELOPMENTAL CHANGES OF PIECES OF FROG EMBRYOS CULTIVATED IN LYMPH.

S. J. HOLMES.

In the course of some experiments on the behavior of the epithelial tissue of frog embryos when cultivated in lymph or plasma it was found that pieces of tissue sometimes underwent developmental changes. During the comparatively short time in which material was available for experimental work, opportunity was not found for devoting as much attention to the changes in these pieces as was desirable. Nevertheless a few of the things observed were sufficiently striking and suggestive to be worthy of record, and it is hoped that the observations may be made more complete at a future date.

The material used consisted of embryos and young larvæ of *Rana* taken out of the jelly a short time before they were ready to make their natural exit. The jelly was placed for a few minutes in an antiseptic solution, and the embryos were afterward cut to pieces in sterile Ringer's solution. Each piece was then mounted in a hanging drop of lymph or plasma of the adult frog, sealed up in a hollow slide, and kept in a cool place. Every few days the piece was transferred to a fresh medium.

Changes in the ectodermic epithelium were quite manifest a few hours after the pieces were mounted, and in one or two days remarkable strands and sheets of ectodermic cells were to be seen extending into the culture medium. These structures and the behavior of their component cells are more fully described in another paper now in course of publication. But aside from the movements of the ectoderm, there were, in certain of the pieces, marked developmental changes of the internal parts. Irregular fragments of tissue frequently became more rounded in form; sometimes they put out lobes or processes of various kinds, and, in some cases, they increased noticeably in size. In a piece from the head region of a late embryo shortly before the rudiments of gills made their appearance, there were developed,

in addition to several larger lobes, a number of finger-like processes which very closely resembled the filaments of the gills. The central part of these projections was composed of connective tissue, and the epithelial covering consisted of a layer of columnar

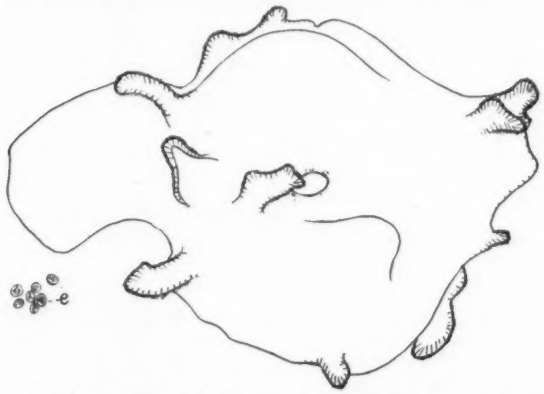

FIG. 1. Piece from the head of a frog embryo drawn fifteen days after being cultivated in lymph. *e*, isolated ectoderm cells.

ciliated cells. These outgrowths began three days after the preparation was made, and they were practically completely formed in a week. Fifteen days after the piece was mounted it had assumed the form shown in Fig. 1. The cilia on the projections were beating, and in fact they continued active for two more weeks, but there was little further change in the general form of the piece. When originally mounted the piece was opaque, and the cells composing it contained a large amount of yolk. After two weeks it had become nearly transparent; the larger part of the yolk in the cells had been assimilated, and a typical connective tissue had developed in the interior from the comparatively unspecialized cells of the mesoderm. The piece was covered completely by ectoderm which, over most of the surface, was flattened, but assumed a cylindrical form on the more prominent projections. In the third week a layer of epithelium was sloughed off from a large part of the surface of the piece.

Whether the finger-like processes represent gill filaments is more or less open to question. Processes of this kind failed to make their appearance from the hinder part of the embryos.

Should they be gill filaments they would afford a case of the self differentiation of an organ in the absence of certain stimuli, such as those afforded by the blood supply, which normally are associated with their formation.

Fig. 2 represents a development from a cross section of a late embryo near the middle of the tail region. This piece, like the one just described, was at first opaque, owing to the large amount of yolk in the cells. A week later it became quite transparent,

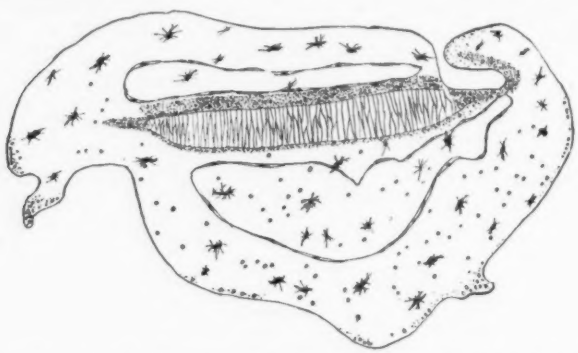

FIG. 2. A cross section from near the middle of the tail of a frog embryo drawn seven days after being cultivated in lymph.

and numerous pigment cells became differentiated beneath the ectoderm. Externally it was completely covered by a layer of flattened epithelial cells. The connective tissue within the piece had become more specialized. At either end of the piece there appeared a prominent outgrowth, the one at the posterior end curving upward and forward. There were two large cavities lined with a single layer of much flattened endothelial cells. These cavities were much larger than any spaces in the original piece of the embryo, and not improbably represent closed and distended blood vessels. The notochord showed at each end an extension of cells which suggested that the organ was undergoing regeneration in both directions. These extensions lay entirely within the new outgrowths from the cut ends of the piece.

Fig. 3 represents a developed fragment taken five days previously from near the middle of an embryo. This piece contained some entoderm which is included in the dark pigmented mass

near the center. At one side there was a thin vesicle filled with fluid. The ectoderm cells covering this vesicle were much flattened. Ten days later the whole piece was larger, owing to the increase in the size of the hollow vesicle which had come to

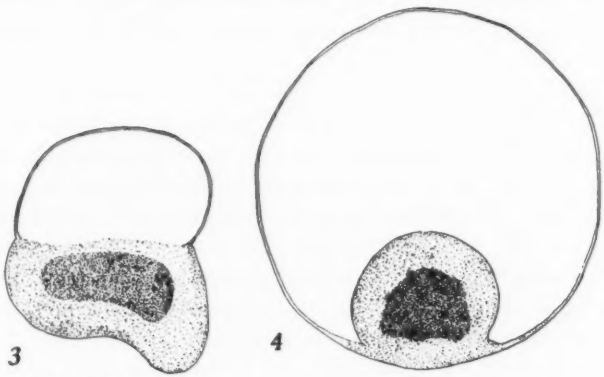

FIG. 3. FIG. 4.

FIG. 3. A piece which developed from a fragment of a middle portion of a frog embryo.

FIG. 4. The same piece as is shown in figure 3, but drawn ten days later.

surround most of the rest of the fragment (Fig. 4). The pigmented mass and the tissue around it had assumed a more nearly spherical form, and the whole structure had become more nearly spherical also. Apparently the chief factor in the form changes in this case was the absorption of fluid which caused the increasing distension of the thin walled vesicle. A similar process may account for the large spaces in the fragment shown in Fig. 2. In transferring the nearly spherical fragment to fresh lymph the thin wall of the vesicle partly collapsed, but it was subsequently distended to its previous form. During the time the piece was kept alive, which was about five weeks, it showed no other marked changes in form.

UNIVERSITY OF CALIFORNIA,
June 16, 1913.

NEMATOLAMPAS, A REMARKABLE NEW CEPHALOPOD FROM THE SOUTH PACIFIC.

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In a collection of Cephalopoda from Sunday Island, one of the Kermadec Group, which has been recently placed in my hands for investigation, is a new oegopsid possessing features of such general interest that the sender of the specimens, Mr. W. R. Oliver of Auckland, has kindly permitted me to offer the following brief preliminary account of the species in an American publication pending the appearance of a full report on the collection in the Transactions of the New Zealand Institute.

Nematolampas regalis new genus and species.

The body is small, cylindro-conical in outline, and terminates in a not very sharp point posteriorly. The fins are very large in proportion to the body, their combined width being as great as the length of the latter, although they are not quite half so long. They are practically continuous with one another above, at least posteriorly, and their union with the mantle is very insecure in alcoholic material. On each side of the extreme posterior tip of the body and lodged in the angle between the fin and mantle is a small swelling containing a conspicuous heavily pigmented body of spherical outline which from its general appearance has undoubtedly a photogenic function. This entire mass with its contained organ is not very firmly attached and becomes readily dislodged when the fins have been loosened.

The head is relatively large, short, and rounded. The eyes are very large. Bordering the ventral periphery of each eyeball is a longitudinal series of five beadlike photophores of a reddish color. Of these the central one is considerably the largest and so conspicuous that it is readily visible through the outer integument. Both it and the smaller organs just adjacent to it are

circular-ovate in outline, but the terminal organs are comparatively narrow and elongate.

The arms are unequal in length, and in one instance, that of the ventro-lateral pair, this inequality is of a very extraordinary nature. This arm pair is in any case the longest and their basal portions much the stoutest, but furthermore each terminates in an exceedingly slender beaded filament which when straightened out is considerably longer than the entire remaining portion of the animal and is devoid of suckers, though the arm proper is normal in this respect. The entire arm bears a succession of small but heavily pigmented photogenic organs scattered at various intervals along its outer margin. On the filament these appear as swellings or tubercles, often half as large in diameter as the filament itself, but on the basal portion of the arm they become rather deeply imbedded and are not easily seen except by transmitted light. Including its filament the better preserved arm of this pair carries a total of thirty-one photophores. The remaining arms are normal as regards their extremities, but those of the dorsal and dorso-lateral pairs bear each a single photophore near the tip. All the arms bear two rows of small suckers, but no hooks. The order of relative length is 3, 2, 4, 1.

The tentacles are about as long as the mantle, their clubs little expanded and armed with four rows of suckers. Each has a pale indistinct swelling in the stalk a short distance from the base and a similar one a little distance below the club. Except that the proximal one is situated considerably nearer the base of the stalk, these swellings occupy a region analogous to the position of the tentacular photophores described by Chun for *Thaumatolampas* (1903, p. 570, fig.; 1910, p. 59, pl. 1–4) and quite likely represent similar structures.

As in *Thaumatolampas* also some of the more important luminous organs lie within the mantle cavity and in the living animal are visible only by reason of the transparency of the pallial tissues. These organs are eight in number and throughout are clearly homologous in the two genera. The two anterior are situated one on either side of the alimentary canal just back of the funnel and correspond to the anal organs of Chun.

In the present form they are quite small. A little behind the middle of the body is a very conspicuous transverse series of five organs. The central one is unpaired. Close to it on each

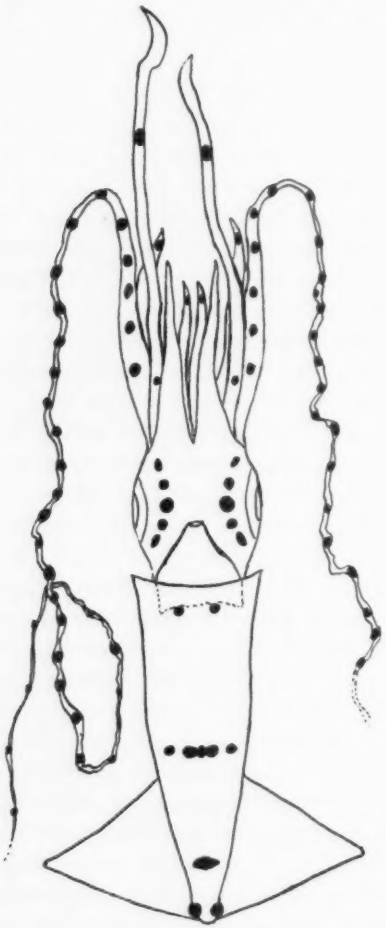

FIG. 1.

side is a very large flattened organ. The terminal organs are the smallest of the series and situated one at the base of each

gill. In the posterior part of the pallial chamber between the fins is a large unpaired organ.

The medio-dorsal length of the mantle is 32 mm., the width of the same 11 mm. The length of the entire animal exclusive of the tentacles and the filaments of the third arms is about 57 mm. The length of the third arm pair is over 70 mm.

From the above account it will be seen that this small squid possesses no fewer than ninety definitely and symmetrically arranged photogenic organs, and it may well be that there are even others which have escaped my search, as the opacity of the tissues in preserved material in many cases renders their detection difficult. Those which I have been able to make out are shown somewhat diagrammatically in the accompanying drawing, and also in the following tabular statement:

Ventral periphery of eyeball	10
Tip of dorsal arms	2
Tip of dorso-lateral arms	2
Ventro-lateral arms	62+
Tentacles	4
Within pallial chamber:	
Anal	2
Branchial	2
Abdominal	4
Posterior extremity of body	2
Total	90

No cephalopod heretofore described is at all comparable to this creature excepting the wonderful *Thaumatolampas diadema* Chun, already mentioned, and the *Lycoteuthis jattai* of Pfeffer ('00, p. 161), both of which are now thought by the latter author to be based upon the same species ('08, p. 294). Chun, in the course of his amazing description of the luminous organs of *T. diadema*, says, "Unter allem, was uns die Tiefseetiere an wundervollen Färbungen darbieten, lässt sich nichts auch nur annähernd mit dem fast magischen Kolorit dieser Organe vergleichen. . . . Es war eine Pracht!" But to judge merely from the anatomy of *Nematolampas*, even *Thaumatolampas* must be outmarveled in life by this wonderful mollusk from the Kermadecs.

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